23(A

University College of Wales

ABERYSTWYTH

Jubilee REPORT of the

WELSH PLANT BREEDING STATION

NSP
RAM
MM

1919 - 1969

COMMONWEALTH MYCOLOGICAL INSTITUTE
13 JAN 1971

Aerial view of the Welsh Plant Breeding Station
Aero Stills Ltd.

Welsh Plant Breeding Station
Aberystwyth

Jubilee REPORT

1919-1969

To be obtained from the Secretary
Price 50 new pence (Post Free)

PLAS GOGERDDAN
Near ABERYSTWYTH
Tel. Bow Street 255-259

Reproduction Rights Reserved

Printed by Welsh Plant Breeding Station
1970

Digitized by the Internet Archive
in 2025

https://archive.org/details/welsh-plant-breeding-station-report_1919-1969

CONTENTS

	Page
List of Staff	1
Introductory Review	5
Research Reports	
Herbage Plant Breeding	11
Grassland Agronomy	48
Seed Multiplication and Herbage Seed Research	74
Arable Crops	101
Developmental Genetics	143
Plant Pathology	168
Chemistry	183
Cytology	195
Physics	208
General Report for 1968 and 1969	215
Meteorological Data	223
Conversion Factors	225
Publications	226

STAFF
(as on 1 January 1969)

DIRECTOR:

Professor P.T.Thomas, C.B.E., B.Sc., Ph.D.

DEPUTY DIRECTOR:

D.J.Griffiths, M.Sc., Ph.D., F.I.Biol

DEVELOPMENTAL GENETICS:

J.P.Cooper, M.Sc., Ph.D., D.Sc., F.I.Biol.
C.F.Eagles, B.Sc., Ph.D.
P.J.Goodman, B.Sc., Ph.D.
I.Rhodes, B.Sc., Ph.D.
K.J.Treharne, B.Sc., Ph.D.

Mrs.J.Charles-Edwards, M.Sc., D.M.Hughes, H.N.C., L.I.Biol., E.J.Lloyd, H.N.C., Mrs.M.J.Mee, B.Sc., F.I.Sant, B.Sc., D.H.Williams, H.N.C.

Scientific Assistants:

M.Collison, Miss J.W.Davies, J.G.Jones, S.S.Mee, R.J.Toler

HERBAGE PLANT BREEDING:

E.L.Breese, B.Sc., Ph.D.
W.Ellis Davies, B.Sc.
Martin Borrill, B.Sc., Ph.D., F.L.S.
A.H.Charles, B.Sc., Ph.D.
M.D.Hayward, B.Sc., Ph.D.
J.Hill, B.Sc., Ph.D.
Elfed J.Lewis, B.Sc.
L.R.Mytton, B.Sc.

D.E.Stephens, B.Sc., B.F.Tyler, B.Sc., D.R.Evans, H.N.C., D.H.Hides, B.Sc., Miss M.Kirby, N.D.D., J.F.Potter, B.Sc., Miss A.C.Thomas, B.Sc., N.R.Young, B.Sc.

Scientific Assistants:

D.W.Bowen, Miss L.Cannon, R.W.Davies, T.R.Elias, W.R.Evans, Miss L.Howells, Miss D.H.Hughes, I.P.Jones, J.L.Jones, H.N.C., Miss Llinos Jones, N.Cert. Agr., G.Leypoldt, R.H.Llewelyn, B.G.Owen, Miss S.Pritchard

GRASSLAND AGRONOMY:

Roy Hughes, M.Sc.
Miss A.G.Davies, M.A., M.Sc.
Ieuan Davies, M.Sc.
D.G.Miles, B.Sc.
J.M.M.Munro, B.Sc., M.Agr.Sci (N.Z.)
Dip.Agric. (Reading)
A.Troughton, M.Sc., Ph.D.

D.A.Davies, B.Sc., W.B.Evans, H.N.C.,
W.H.Rushton, H.N.C., R.G.Simons, B.Sc.,
R.J.K.Walters, B.Sc., I.G.Williams, B.Sc.

Scientific Assistants: Miss Cecilia Badger, J.H.Davies, E.M.Evans, H.N.C.,
Miss C.Evans, Miss J.Harries, Miss E.Jones, E.L.Jones,
J.R.Jones, C.J.Mee, T.E.H.Morgan, J.W.Payne

SEED MULTIPLICATION AND HERBAGE SEED RESEARCH:

D.J.Griffiths, M.Sc., Ph.D., F.I.Biol.
H.M.Roberts, B.Sc.(in charge of Seed Mult.)
E.W.Bean, B.Sc., Ph.D.
J.Lewis, B.Sc., M.I.Biol.
J.L.Stoddart, B.Sc., Ph.D.

T.B.Edwards, H.N.C., T.W.A.Jones, B.Sc.,
R.A.D.Pegler, B.Sc., M.I.Biol.

Scientific Assistants: W.J.Evans, P.E.Evans, Mrs.S.Hobson, Mrs.J.Lloyd,
J.J.Powell, I.Williams

ARABLE CROP BREEDING:

J.D.Hayes, B.Sc., M.S.(Wisconsin), Ph.D.
J.Cotten, B.Sc., Ph.D.
B.C.Clifford, B.Sc., M.S., Ph.D.
T.D.Johnston, B.Sc.
D.A.Lawes, M.Sc.

D.L.Jones, H.N.C., Idris Jones, I.T.Jones, M.Sc.,
D.A.Lewis, H.N.C., P.A.York, B.Sc.

Scientific Assistants: R.Davies, W.Davies, T.E.R.Griffiths, J.E.Jones,
Mrs.S.Jones, W.Jones, Miss M.Joyce, Mrs.D.A.Ralphs

PLANT PATHOLOGY:

A.J.H.Carr, B.Sc., Ph.D.
John A'Brook, B.Sc., A.R.C.S., D.A.S.
(Cantab), D.T.A. (Trinidad)
P.L.Catherall, B.Sc., Ph.D.
P.W.Wilkins, B.Sc.

Scientific Assistants: Miss M.Jones, L.R.Potter, J.A.Watt

CHEMISTRY:	D.I.H.Jones, B.Sc., Ph.D. R.Welch, B.Sc.
	T.A.Thomas, H.N.C.
Scientific Assistants:	Miss M.Crees, J.S.Harries, Miss J.G.M.Jones, Miss E.Rowlands
CYTOLOGY:	Professor P.T.Thomas, B.Sc., Ph.D., C.B.E. Hugh Thomas, B.Sc., Ph.D. D.H.Clapham, B.A.
	J.Clarke, M.I.Biol., Mrs.J.Mytton, H.N.C.
Scientific Assistants:	W.G.Morgan, Miss Linda Hall, Mrs.J.V.Stowe, Miss A.L.Williams
PHYSICIST:	F.H.Vanstone, B.Sc., Ph.D., A.Inst.P.
	A.V.Fall, H.N.C.
Scientific Assistants:	T.E.Williams, D.Mason
SCIENTIFIC LIAISON AND VISUAL AID:	Ll.Iorwerth Jones, B.Sc. Llywelyn Phillips, B.Sc. R.M.Thomas (Special Assistant) J.H.Richards (Photographer)
MINISTRY OF OVERSEAS DEVELOPMENT:	J.B.Abington, B.Sc. C.A.Foster, B.Sc.
TECHNICAL:	Evan T.Jones (Technical Works)
ACCOUNTANT:	J.D.N.Humphreys, A.C.C.S.
EDITOR OF PUBLICATIONS:	Mrs.E.Horzelska
STORES:	B.R.H.Rowlands
LIBRARIAN:	Miss J.M.Williams
CLERICAL OFFICERS:	Miss A.Budge, J.Forsyth, D.A.Isaac, Mrs.D.Lewis, Miss H.M.Pierce, Mrs.G.M.V.Pritchard.

TYPING STAFF:	Mrs. J. Flindall, Mrs. R. A. Hemingway, Mrs. L. Jones, Mrs. H. M. Lawden, Miss S. Mee, Mrs. S. B. Morgan, Mrs. H. M. Rowe, Miss J. V. Turner, Miss K. M. Williams.
ASSISTANT STOREMAN:	R. Parrott
TELEPHONE OPERATOR:	G. T. Michell
MACHINE OPERATOR:	Miss E. Roberts

SECRETARY

J.W. Ellis, D.P.A., A.C.I.S.

FIFTY YEARS PROGRESS AT THE WELSH PLANT BREEDING STATION

INTRODUCTORY REVIEW

In this enlarged report, associated with the fiftieth anniversary of the founding of the Welsh Plant Breeding Station at Aberystwyth, an attempt has been made to review some of its past work and achievements, to report on current investigations, and to define policy and objectives in relation to future developments in agricultural research.

Many of the agricultural research institutes in Britain were founded through the missionary zeal of individuals and the munificence of generous benefactors. Thus the Welsh Plant Breeding Station was established in 1919 with an initial gift of £10,000 from Lord Milford and a further contribution of £1000 a year for ten years. Likewise, in March 1933, Sir Julian Cahn made available to the Station a fund of £3000 per annum for seven years for the establishment and maintenance of the Cahn Hill Improvement Scheme.

The first Director of the Station, Sir George Stapledon, was also Professor of Agricultural Botany at the University College of Wales, Aberystwyth, and the close link between teaching, post-graduate training, and the more applied aspects of research continues to be maintained. Although basically the Station remains as a research department of the College, during the 50 years of its development it has become recognized as a major research institute and is now fully grant-aided by the Agricultural Research Council.

Stapledon's pioneer work was started with very modest facilities, but these mattered less in relation to his tremendous enthusiasm and the dedication of a small group of scientists on the staff who were to make a significant contribution to plant improvement. They included T. J. Jenkin (Grass Breeding, and Director 1942-50), E.T.Jones (Oat Breeding, and Director 1950-58), R.D.Williams (Clover Breeding), William Davies (Grassland Agronomy, and later Director of the Grassland Research Institute, Hurley 1942-68), and Gwilym Evans (Seed Multiplication, and Deputy Director 1957-61).

The objectives of the Welsh Plant Breeding Station were clearly defined due largely to the urgent need to improve the grasslands of this country. They were in such a state that apart from a few so called "fattening pastures" the emphasis was clearly on maintenance rather than on production. Indeed there was little incentive to treat grass as a productive crop, because imported concentrates were available at very cheap rates. A 'bumper' crop of hay was considered desirable and this was harvested at a mature stage of growth to provide the roughage component of winter fodder. Farmyard manure was applied after hay, and sometimes basic slag on grazed pastures to promote the growth of clover.

During the 1914-18 war so much land was ploughed up for cereals that the country was faced with the serious problem of re-establishing reasonably good pastures. It was

well-known that it took many years for a sown pasture to develop into a sward that was as productive as the original ploughed up permanent pasture. Not only were the seeds unreliable, being of unspecified origin, germination and weed content, but the established plants were stemmy and short-lived. After the initial flush of growth the sward soon became very thin and weedy, and by the second or third year, the sown species had disappeared almost completely. Under these circumstances indigenous grass and clover were able to establish and these were clearly better adapted to the environmental conditions prevailing on the farm.

These adapted indigenous species of grasses and clover formed the basis of herbage plant breeding at the Station. Plant material was collected from a wide range of environments and, especially, from productive pastures which had been subjected to different management. In this way the now well known series of S varieties were produced. Within each species, a number of varieties with different growth rhythms were established, but they all had the characteristics of being more leafy and persistent than the commercial types.

Selection for these desirable vegetative characteristics was naturally associated with some loss of seed potential, and therefore serious consideration had to be given to the agronomy of seed production. The successful promotion of these new leafy varieties was greatly facilitated by active collaboration with seed growing farms and the seed trade, resulting in what amounted to a new seed industry in this country. To ensure promotion of authentic high quality seed, the Station also pioneered the development and operation of a seed certification scheme, ultimately evolved into the present British Comprehensive Certification Scheme for Herbage Seed.

The introduction of the S varieties was a notable land mark in the history of grassland improvement, but their impact on production would probably have been minimal if the Station had not given close attention to the problems of agronomy for effective management. In many ways these varieties were ahead of their time, because the standards of management and level of fertilizer application were far too low. Comprehensive agronomic trials, using animals as far as possible, showed conclusively that each variety or combination of varieties must be specifically managed in order to take full advantage of their superior attributes.

In recent years technological advances, associated with good farm advisory service, have led to a greater appreciation of these varieties, especially at high stocking rates and levels of fertilizer application. The high-tillering persistent forms come to their own under these conditions and are responsible for the development of productive long leys which, under favourable conditions of soil, climate and satisfactory management, are now often classified as permanent pastures.

The Station has always given close attention to the problem of improving permanent pastures, especially in upland areas, and clear principles have been established. From this work we can now confidently generalize that any permanent pasture can be upgraded by management and fertilizer application alone, but the nature and speed of the improvement will differ in a manner that can be clearly predicted. In this way,

at the lower level of fertility, a Nardus/Molinia sward can be manipulated to give at least a 10-fold increase in production. But this is achieved not by a direct response of the original sward, but by a gradual change in the botanical composition through the natural introduction of lowland species, and the result is the production of a reasonably good grass/clover sward within a period of up to 20 years. With bent/fescue pastures there is some direct effect, but a significant improvement is again only achieved by the same slow process leading to a change in botanical composition.

More dramatic improvements can, however, be immediately achieved by reseeding after appropriate cultivation and fertilizer application. Moreover, when it was possible to completely destroy the native herbage, it has been shown that varieties used for these pastures can persist for over twenty years. This is important, because under unfavourable upland conditions the unproductive native herbage will cause reversion as soon as the standard of management is relaxed. It is, however, difficult for a hill farmer to adopt the more intensive lowland methods of management, and current work at the Station is directed towards the development of productive varieties which are better adapted to the less favourable conditions prevailing on the uplands. In specific terms, it is important to establish and maintain clover not only because of its nutritional superiority, but because of the doubtful economic value of increasing production by application of nitrogen.

The principles established for the improvement of upland areas apply equally well to lowland pastures, but on the latter response to fertilizer application is more significant, improvement can be effected relatively more quickly, the potential is higher and the improved sward more stable. Again, it is a dynamic situation in that there is a change in botanical composition towards ryegrass. Moreover, the type of ryegrass which develops will depend precisely on the system of management. Thus, with intensive close grazing, the prostrate perennial form will predominate, but any system of management which includes conservation, especially at a late stage of growth, will favour the more erect type which has been found to be less persistent in the absence of cycling of nutrients through the animal. Thus, we have been able to provide a blueprint for the direct improvement of permanent pastures, and it only remains for the farmer, with the help of the advisory service, to put this into practice.

What has so far been achieved, whether through breeding or by ecological manipulation, is to provide pastures which are able to satisfy most of the demands of present day farming practice, and the emphasis has naturally been on factors which will enhance agronomic performance. The next challenging phase is to associate agronomic performance in herbage with a new range of factors which are important for maximum animal production per unit of land, and this is where a state research institute has a vital role to play through advanced methods of plant breeding.

Under these terms of reference we appreciate that grass is a very complex crop, especially in comparison with agronomically simple arable crops in which the parts of the plant which are economically important (grain, tuber root etc.) are well defined, have reasonably consistent chemical composition, and are harvested only once during

a season. With herbage crops, on the other hand, nearly the whole of the above-ground part is harvested many times during the year, and both the yield and chemical composition are materially affected by management. Further significant advances in their breeding can, therefore, only be expected when carried out against a background of these major considerations.

Although good commercial varieties can still be produced by empirical methods, it is vitally important that a research institute should devote most of its efforts towards achieving major objectives which will have a significant impact on future advanced systems of agriculture. To this end the plant breeder can no longer work in isolation, but must collaborate closely with a number of scientific disciplines which alone can provide the necessary techniques for effective progress.

Basically we are concerned with the problem of efficient conversion of solar energy and soil nutrients into the kind of fodder needed by the animal for maximum production, and the following three questions are important considerations:

(1) What is biologically possible?
(2) What is scientifically and technologically attainable?
(3) What is economically significant?

An important step in these directions was made in 1959 when a department of Developmental Genetics was instituted whose primary task was to assess the amount of genetic variation present in breeding material for those physiological characters which are significant for ensuring an adequate and continuing supply of quality herbage. It was soon realized that the biological potential of grass is significantly higher than any single arable crop. Moreover, it was shown that there is tremendous genetic variation for productive and nutritive characteristics which would enable the breeder to develop improved varieties. These include photosynthetic efficiency and growth at varying temperatures and water-stress, reaction to cold, uptake and utilization of minerals, as well as chemical constitution and physical characteristics. A comprehensive genetic survey of these and other physiological and biochemical processes is giving us, for the first time, a more precise indication of what is biologically possible in herbage plants, and we may confidently look forward to the development of new types of varieties whose increased potential can be fully achieved under more advanced and specialized systems of farming.

Research in agronomy holds a central place in guiding the plant breeder on the model of variety which is likely to be successful under future systems of farming, and especially in association with researches in nutrition chemistry, the constitution of a variety which will give maximum animal production. Thus, it has been possible to establish a precise code of management which will avoid or minimize winter-kill in a type of variety which excels in autumn production, and to indicate the degree of dormancy required for varieties to be grown under more rigorous winter conditions. Likewise, the agronomist is engaged in understanding some of the problems. such as poaching and soil compaction, associated with intensive grazing at heavy stocking, and to distinguish the type of variety which can withstand these conditions.

Apart from being able to breed cocksfoot to the same level of digestibility as ryegrass, perhaps the most striking feature of the work on factors affecting animal performance is the demonstration that clover is nutritionally complementary to grass which by itself can be seriously deficient in minerals at high levels of animal production. For meat and wool production the nutritional superiority of clover can be attributed both to organic and mineral constituents. In confirmation of the conclusions, significant differences have been found between species, varieties and genotypes of grass in respect of both quantity and availability of minor elements like cobalt and copper - differences which are reflected in voluntary intake and animal production at equivalent levels of digestibility.

Our objective with regard to herbage breeding is clear - that of combining improved nutritional characteristics with high agronomic performance. Success in this direction will depend on being able to acquire a large store of genetic variability and to develop efficient techniques of manipulation to establish the best combination of characteristics. In recent years the Station had made extensive collections of plant material from widely different environments, covering virtually the whole of Europe and N.Africa. Selected plants from these collections are continually being incorporated in the breeding programmes to provide promising potential varieties, some of which are already being introduced on the market. Naturally, the greatest effort is being devoted to those species which are of particular significance to British agriculture and here the ryegrasses take pride of place. A major objective is to introduce some of the attractive nutritional and other characteristics of Italian ryegrass into the persistent forms of perennial ryegrass which have high agronomic performance. These two species have already been combined successfully as fertile stable allotetraploids, and new varieties are being released to commerce. Further progress in this direction will involve the development and use of more sophisticated techniques of chromosome manipulation in order that the best characteristics of both species may be effectively combined.

The hexaploid tall fescue has been found to have a very high biological potential, and a more ambitious programme at the Station has been to introduce chromosomes from the diploid ryegrasses, especially Italian ryegrass. Again, reasonably fertile allopolyploids have been produced and attractive derivatives, especially suitable for conservation, have been obtained.

Although the research work at the Station has been mainly on pasture improvement, close attention has also been given to the arable crops which can appropriately be grown in the western half of Great Britain. Initially, the emphasis was on the oat crop - especially winter oats - in which an outstandingly successful series of varieties has been produced.

The biological potential of arable crops is at least as high in the west as in the east, but we are concerned with a different spectrum of factors, notably diseases which make it more difficult to achieve this potential as harvestable yield. Experience with the oat crop has shown the value of breeding for disease resistance, particularly when

we realize that barley was virtually free of disease before it became intensively grown. Indeed, we have now reached a stage where the actual grain yield of oats is shown in national trials to be higher than that of barley. Naturally, under these circumstances, the work both on oats and barley is at least as much concerned with factors which limit production as with increasing biological potential and grain quality of the crops.

As with pasture plants, the policy of the Station is to investigate a wide range of fundamentally important problems and to develop advanced techniques of breeding for the benefit of all who are engaged in the production of higher yielding varieties. They include:

(a) studies on the genetics and nature of disease resistance;
(b) identification and significance of pathogens, especially viruses, which affect both grass and cereals;
(c) the relative importance of pests, like cereal cyst nematodes, in relation to breeding for resistance;
(d) genetic variation for reaction to herbicides, pesticides and fungicides;
(e) appraisal of the role of hybridity and the development of techniques for economic exploitation;
(f) changing the breeding system of a crop like beans for more consistent production;
(g) chromosome manipulation as a means of introducing desirable characteristics from wild species into improved and adapted cultivated varieties;
(h) production of independent plants from gametophytic material for the production of homozygous varieties.

All these are problems which would not be readily studied by private plant breeders because of the demand for sophisticated resources and time consuming research effort which will not be immediately rewarding financially. They are, however, of vital importance for significant advances in plant breeding. Active liaison and collaboration between private and state breeding organizations will inevitably lead to a new era in the production of improved farm crops for a more prosperous agriculture.

P.T.Thomas

Director

HERBAGE PLANT BREEDING

E. L. BREESE

W. E. DAVIES

The early advances in herbage plant breeding owed much to the development of sound ecological principles and to their use in exploiting naturally occurring adaptations. Ecological studies led to a consideration of the control of variation through the breeding system. The outbreeding nature of the main agricultural species was soon recognized and principles for variety construction and maintenance during seed multiplication as well as techniques for controlled hybridization were quickly evolved. This led to the production of varieties which have had a profound effect on British agriculture, and in many instances still have a potential which is far from being fully realized under existing farm practice.

These varieties were not produced without a full appreciation of the complexity of the crop. Unlike arable crops, grassland species are harvested many times during the year, either directly by the animal or by a system of cutting and conservation. Furthermore, most of them are perennials expected to yield continuously for a number of years and over a range of soil types and climatic conditions.

Clearly, the complexity of the crop presents many problems both in management and utilization which require the concerted effort of many disciplines. This has led to a multi-discipline approach to improvement by breeding. A review of the early history of the breeding work will reflect the development of this approach and trace the origin of the research studies at present undertaken by the department.

THE EARLY YEARS 1919-1939

In these early years the history of the Herbage Breeding Department (grasses and legumes) is inseparable from that of the whole Station. Advance was largely pioneered by the first Director, R. G. Stapledon, ably supported by his colleagues T. J. Jenkin (on grasses) and R. D. Williams (on herbage legumes). Before 1919 little was known about the common agricultural grasses and legumes, and a first requisite was the collection and evaluation of local and regional races of grassland species.

By these methods the more productive species were recognized, but more importantly, an appreciation of the wide range of variation within a species was obtained. A study of this variation led to the concept of plant types being associated with particular

kinds of agricultural and natural habitats. This concept of species becoming adapted to specific ecological conditions (termed 'ecotypes') was also developed in ecological studies by Turesson, Gregor and others. The idea followed that particular growth forms were valuable in relation to particular agricultural purposes, and improvement of regional strains by selection of the more desirable forms marked the beginning of the breeding programmes.

In the meantime T. J. Jenkin, A. R. Beddows and R.D.Williams had undertaken an intensive study of the breeding systems of the various grasses and clovers, the results of which were summarized in Station Bulletin H.12 in 1931. Recognition of the essentially outbreeding nature of the more important species made it possible to lay down the principles for maintaining genetic purity during the multiplication of seed stocks and to develop techniques for controlled hybridization (23). This led to a study of incompatibility systems in the clovers, and to the commencement of an extensive investigation into species relationships and the production of interspecific hybrids in grasses.

In 1933, Stapledon wrote an account of organization and work of the Station 1919-1933, in which he stressed the need for clearly defined agronomic objectives as the prerequisite of plant breeding. He firmly linked the principles of grassland management and utilization developed from agronomic and biochemical studies (reported elsewhere in this issue) with breeding objectives. Thereby he secured the basis for the coordinated pattern of multi-discipline research and development which is so much a feature of the Station's present policy.

These twenty years provided a firm foundation for future progress, and during this period many of the present well known S varieties were developed and fourteen released to the seed trade.

INTERIM YEARS 1939-1959

The outbreak of war in 1939 had a two-fold effect on the Station's herbage breeding activities. The sudden desperate need for home grown production caused a revolution in agriculture in which the principles and practice of grassland management and utilization developed at the Station played a role so significant that it is now a matter of national record and accord. This role could only have been fulfilled because appropriate varieties were already developed at the Station and the national crisis gave the impetus to the production of increasing quantities of seed, again developed as a home industry. The war and post-war years completely vindicated the approach of the Station to grassland improvement, and irrevocably established grass as a crop of major economic importance.

On the other hand, research and breeding programmes came to a standstill. Most of the Station staff were seconded as technical officers to regional War Agricultural Committees and Station activities were reduced to a care and maintenance basis. The effects of this cessation of research and development were to extend well into the post-war years, since, as pointed out by E. T. Jones in 1955 (27), "plant breeding research

cannot be discontinued and again after an interval of a few years be resumed at the point where it was left off". The clover programme suffered a further setback when R.D.Williams died suddenly in 1943. This loss was the more severe in that there was no-one left with an intimate knowledge of the legume breeding material collected over 20 years.

Post-war breeding and research programmes in grasses recommenced under A.R. Beddows (36). A first consideration was to extend the search for naturally occurring variants within the more important grass species, and to screen collections for valuable breeding material. Collections were also made of genera not normally used in current agricultural practice in the United Kingdom such as Holcus, Anthoxanthum, Phalaris, Agrostis, Poa and Alopecurus. Previously the emphasis had been on the improvement by selection of indigenous material naturally adapted to our own climatic conditions. But at that time a major objective of the breeding programme was to obtain a longer period of growth throughout the year. Consequently, the search for new material was extended to southern and western Europe in an attempt to discover geographic races of the more important grassland species which might have become adapted to growing earlier or later in the season than indigenous material. The search was highly successful and was to mark the beginning of an extensive plant introduction programme.

The greater proportion of the first introductions were Dactylis populations, many of them obtained from Mediterranean habitats. Their study was undertaken by M.Borrill. A number of them were discovered to have useful agronomic characters, particularly in exhibiting growth potentials for out of season production. Race and species relationships were investigated in conjunction with K. Jones of the Cytology Department, and the presence of diploid and tetraploid populations was discovered. This began a most profitable association between breeders and cytologists which was to extend to the investigation of other genera, including Agrostis, Anthoxanthum and the Lolium/Festuca complex of species. These joint studies have yielded information which has paved the way to a determinate exchange of genetic material between wild and cultivated forms and to the production of new hybrids.

Detailed descriptions of interspecific and intergeneric hybrids in Lolium/Festuca and other species were published by T. J. Jenkin in an extensive series of eighteen papers (22). Gradually the effort became intensified on those which showed the greater agronomic promise and these were concentrated in the Lolium/Festuca complex. E.J.Lewis took over the responsibility for the development of intergeneric crosses within this complex and was able to produce fertile amphidiploids by the use of colchicine techniques.

The work with herbage legumes was resumed under Watkin Williams and subsequently (post 1950) under W.E.Davies. An immediate outcome was the successful analysis of data collected by the late R.D.Williams on the genetic control of the mating system in red clover. Compatibility of matings was shown to be controlled by a multi-allelic, single locus system (the S locus), with a large number of different alleles carried in all populations analysed (35). A similar situation was found to exist in alsike clover (Trifolium hybridum).

Work on plant collection and introduction paralleled that in the grasses. For white clover it was deduced that this species had spread northwards in relatively recent times from a centre of origin in Mediterranean regions. Clines of variation could be traced from south European to northern latitudes. Thus Daday (11) in studying variation in the HCN reaction, showed that populations from the supposed centre of origin contained predominantly positively - cyanogenic plants, but that this proportion declined to zero with decreasing winter temperatures. Subsequently it was shown that cyanogenic plants had a disadvantage at low temperatures, while acyanogenic plants are selectively grazed by slugs, hares and rabbits which may confer an advantage to cyanogenic forms where winter cold is not a problem. The precise function of the glucosides predisposing the HCN reaction is however still not known.

A cline in leaf size is also apparent, with northern populations (including British) being uniformly small, while populations towards the gene centre include many with large leaves and long petioles. These have been used in the breeding programme to improve the yield and competitive ability of indigenous varieties. They also provide a source of genetic material for extended autumn growth.

An extensive study of interspecific relationships leading to the production of interspecific hybrids, was undertaken by Alice Evans in the genera Trifolium, Medicago and Lotus (17). Dr. Evans also initiated work on the production of autopolyploid forms (18, 14).

During this period, the need for a more precise evaluation of the breeding material for both grasses and clovers was steadily becoming more obvious. The quantitative characters important in agricultural production (yield, etc.) are subject to environmental modification. Assessment of individual spaced plants does not necessarily, therefore, reflect their true order of merit under competitive conditions in dense swards. An investigation of density dependent interactions among grass varieties was begun by A. Lazenby (continued subsequently at Cambridge with H. H. Rogers) who compared yields under spaced plant, drills and sward conditions (28). Changes in the order of yield did occur, although the extent of this was not considered serious at the time.

Density dependent interactions were also demonstrated for yields among lucerne varieties. In the white clover breeding programme, possible genotype interactions with companion grasses were taken into account by oversowing spaced plants with a companion grass (15). Yield interactions of grass and clover varieties with other management and environmental factors were also closely studied. In the grasses, particular attention was paid to meso-climatic and management influences on the timing of inflorescence production, and to the control of anthesis by the meteorological factors. At the same time a start was made by P. B. Vose on a detailed analysis of the physiological basis of yield, particularly of the nutritional responses and requirements of Lolium perenne populations.

Genetic studies started early in the Department's history and included the control of incompatibility and leaf markings in clover, chlorophyll deficiencies and anthocyanin

production in grasses. The effects of inbreeding on the cross-breeding grass and legume species were well appreciated, and T. J. Jenkin formulated principles for the construction of varieties accordingly. These synthetic varieties were based on a nucleus of selected plants sufficient in number to avoid harmful inbreeding and thus preserve heterozygosity when multiplied in isolation over 3-4 generations. The genetic constitution of the basic plants was determined by progeny testing, usually by a polycross technique, so that plants with good general combining ability were used. The optimal number of basic plants was determined by experiment where numbers from 4 to 8 were indicated, depending on the range in combining abilities of the parents.

In the early 1950s advances in biometrical analytic techniques, developed particularly at Birmingham University Genetics Dept., made possible a more thorough investigation of the genetic control of quantitative characters. Consequently, appropriate mating designs (in particular the diallel cross) to which the techniques could be applied were adopted in certain grasses and clovers. This approach marked the beginning of a comprehensive investigation into the genetic control of production characters and the genetic architecture within the species.

CURRENT RESEARCH AND DEVELOPMENT

By the early 1960s it was becoming apparent that further significant advances in herbage plant breeding could only derive from sound basic research in disciplines giving more emphasis to the efficient conversion of solar energy and soil nutrients into the kind of herbage needed by the animal for optimal production. This entails the necessity to translate the requirements for a herbage variety into physiological and biochemical terms. In order to ensure the effective application of such criteria to plant improvement, it became essential that work in the breeding department should be organized to secure maximum collaboration with scientific disciplines in other departments.

As its primary concern, the Department has undertaken research into improved breeding methods, with regard to both generating and controlling genetic variability. Investigations fall into four groups which are listed under the following headings:-

Sources of genetic variability
Population studies and the genetic control of variability
The grass/clover balance and clover/rhizobia associations
Operational breeding

If the results of scientific enquiry and investigation are to achieve practical significance, it is essential that research and development are closely integrated. In this context the Department assumes a centralizing role within the Station's activities. Material with unusual potentials deriving from the above investigations is developed in association with the Agronomy Department, so that appropriate techniques for utilization in a farm system can be simultaneously evolved. Close collaboration with other Departments is maintained in adopting new screening techniques to breeding routine,

and in further developing material of known physiological and biochemical characteristics.

During the last 50 years, experience in research and in farm practice has gradually narrowed the range of species which are adjudged useful. Today ryegrasses are pre-eminent under intensive animal systems, with the fescues and timothy being relegated to special purposes. The use of cocksfoot has decreased dramatically in the last two decades. Of the herbage legumes, white clover is by far the more important, particularly for the extensive grassland systems of the western parts of Britain. The recognition of the superior value of this restricted range of species is reflected in the research breeding programmes. It allows more intensive investigation to be carried out and, as will be seen, this has led to an appreciation of the tremendous wealth of genetic variability that is contained, for instance, in the Lolium/Festuca complex of species, together with the potentiality for genetic exchange that exists within this group. Although possibilities in other species are not ignored, it may be that this group has the potentiality to provide most of the foreseeable requirements of grassland farming.

Sources of genetic variability

1. Plant introduction

A plant introduction unit was formed in 1962 to survey and conserve genetic stocks of certain wild grasses and legumes which could provide a reservoir of genetic variation for breeding and investigational purposes. During the decade seven expeditions have been organized from the Station, some of them conjointly with research institutes in Britain and overseas. The search was aimed at obtaining a wide range of adaptations to diverse climatic conditions among species which have agronomic importance in the British Isles. Extensive collections of ryegrass, fescues, cocksfoot and clovers, as well as representatives of other species, were made in Iberia (1961, 1963), North Africa (1962), South Eastern France (1962), Scandinavia (1965) and Northern Italy (1967). The publication of seed exchange lists further facilitated exchange between collection centres, and through collection and exchange over 1500 populations of grasses and legumes have been available for observation at the Station.

B. F. Tyler has developed methods for screening and classification. Initially the populations are screened under field conditions (as spaced plants or drills) by a technique which allows some 200 populations to be handled annually (39). Emphasis is placed on obtaining accurate assessment of the pattern of growth throughout the year, but disease resistance, reaction to winter conditions and other potentially useful characteristics (e.g. digestibility) are recorded. Coincidental chromosome studies are carried out in conjunction with the Cytology Department. After classification, selected populations may undergo further physiological investigation, become the subject of genetic study, or enter directly into breeding programmes.

An adjunctive study in this programme is to discover the way in which species adapt to different climatic conditions. Sufficient data are now available to generally cor-

relate growth and other attributes to gross geographic parameters.

Correlation between plant reactions at Aberystwyth and gross environmental parameters at place of origin

		No. of populations	Correlation coefficient r ($P < 0.001$)
Dactylis glomerata	Autumn growth v Altitude (French Alps)	29	-0.650
Dactylis glomerata	Autumn growth v Latitude	56	-0.748
Lolium perenne	Winter survival v Av. lowest temp of coldest month (30 years av.)	16	-0.798
Dactylis glomerata	Rust severity v Altitude (French Alps)	29	0.650
Dactylis glomerata	Rust severity v Latitude	56	0.737

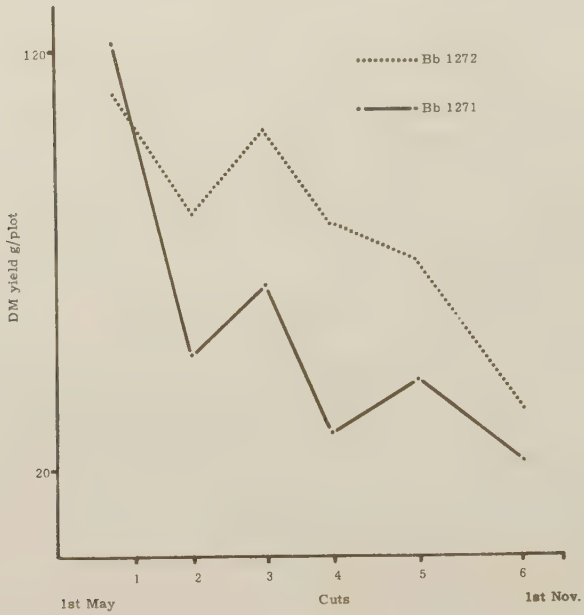
They show quite clearly the strong negative correlation between autumn growth and latitude or altitude of origin for Dactylis populations. This, no doubt, reflects the increasing tendency to early winter dormancy as the original habitats are subjected to lower winter temperatures due to a northwards distribution or increasing height above sea level. Also shown is a parallel relationship with regard to winter survival in Lolium populations, with populations from warmer regions (southwards or lower elevation) being increasingly susceptible to winter kill. A similar relationship appears to hold for Dactylis. This of course, is probably an example of the general role of dormancy in survival. A more detailed examination of representative populations has been undertaken by J. P. Cooper and his colleagues (Developmental Genetics report). To the breeder it represents a challenge to combine a faculty for good growth with acceptable survival risk, - a challenge which has in part been successfully met through hybridization programmes (described later).

An interesting relationship between latitude and altitude and resistance to infection late in the season by striped rust (Puccinia striiformis) on Dactylis is also shown in the table, with the greater tendency to dormancy being accompanied by greater susceptibility to infection. The exact reasons for this are not known, but it raises a fine point in epidemiological considerations. It would suggest that either habitats which evoke dormancy responses are largely free from the pathogen and that selection has not thus operated on the production of resistant genotypes, or that infection of senescing top growth during the pre-dormancy period is of little physiological conseqence to the plant.

The above are examples of gross adaptation to macro-climatic factors, but the ecological conditions at the site of collection can be equally important. Thus, for example, two populations of ryegrass were collected from two sites separated by only

a few miles in northern Italy. Population Bb 1271 was collected from non-irrigated land, while Bb 1272 came from an irrigated meadow. The response of the two populations under conditions at Aberystwyth, where summer water stress is not normally a limiting factor, is shown in the following figure:-

Fig. 1. Seasonal growth of two populations of Lolium multiflorum from northern Italy



Bb 1271 demonstrated the early season growth and the depressed summer yield typical of plant types adapted to summer drought, whereas Bb 1272 showed no such inherent limitation and, indeed, outyielded some of the best existing cultivars by over 25% on a seasonal total. The winter reaction of these populations still has to be evaluated, but they clearly point to the value of naturally occurring variants as raw material for the breeder. At the same time a study of the association between climate, habitat and plant performance provides the surest guide for economical planning of future collecting expeditions.

2. Identification of taxonomic classification

Routine identification and determination of chromosome number is part of the plant introduction scheme. Most attention has been devoted to geographical collections of Festuca and Dactylis. A great deal is now known about species relationships in cocksfoot, and here the main task lies in locating and describing as geographical subspecies the remaining sources of diploid material. In Festuca arundinacea (sensu lato) the main

interest centres on the classification of the numerous chromosome races discovered by recent plant exploration (2). These studies indicate a close relationship with species in section scariosae and indirectly with section montanae. This new information will eventually provide the basis for new taxonomic treatment centred on the Moroccan material, since the limits of some generic sections and our concept of F. arundinacea must now be revised.

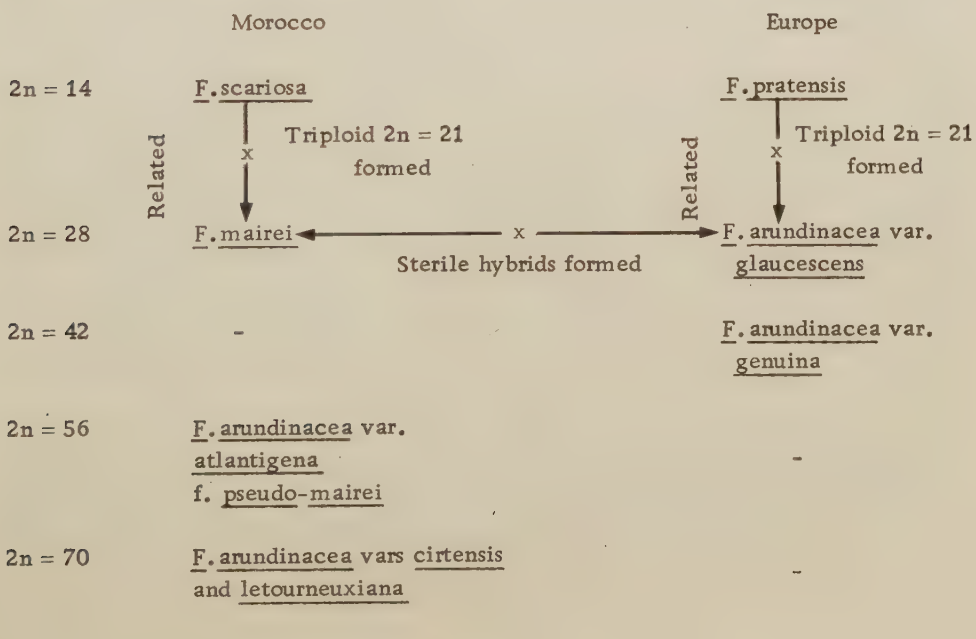
3. Race and species relationships

M. Borrill and E. J. Lewis have continued and developed their investigations into the possibilities for genetic exchange in Festuca, Lolium and Dactylis.

(i) Festuca

Problems associated with the hybridization of hexaploid tall fescue and ryegrass have focused attention on the nature of the species F. arundinacea, its origin and relationships. The plant introduction survey shows that hexaploid tall fescue is the predominant chromosome race in all areas of natural distribution, excluding Morocco where it is replaced by decaploid (2n = 70).

A good deal of attention has been devoted to the Moroccan material because of its distinctive morphology (38). In the summary scheme shown below, it can be seen that the tetraploid F. arundinacea var. glaucescens of S. Europe is replaced in N.W. Africa by the tetraploid species F. mairei, with which it will hybridize. One of the parents of F. mairei is the diploid F. scariosa endemic in the Spanish Sierra Nevada. Both these plants are usually classified in the generic section scariosae (F. arundinacea is placed in section bovineae).



The chief characteristic of the higher polyploids in Morocco (2n = 56, 70), namely increased xeromorphy (expressed in alternate sized leaf ridges and other characters), which sets them apart from the rest of the F. arundinacea complex, is due, it would seem, to the inclusion of the F. scariosa genome in their basic chromosome set.

Elucidation of the genomic basis of Eurasian hexaploid arundinacea is made more difficult by the paucity of putative diploid genome-donors, apart from F. pratensis. Links may be found eventually via the tetraploid chromosome races in arundinacea. Hexaploid F. arundinacea itself occurs in geographically diverse forms, some of which fail to produce fertile hybrids when artificially crossed (Lewis, 37). Morphological differences accompany some of these, for example collections from N. W. Spain are rhizomatous and the Tunisian material has a softer and perhaps more palatable leaf. Principle component analysis has proved useful in diagnosing which characters best determined the extent and distribution of the main sub-groups (1). These studies are being complemented by analysis of diallel crosses between representative populations.

(ii) Dactylis

Dactylis has a very wide geographical distribution and ecological adaptability. Our ability to utilize this natural variation depends on a knowledge of race and species hybridization. Cocksfoot is native in Europe, Asia and the Mediterranean region. Most of the material is polyploid, but many pockets of relict, ancestral diploids are found within this distribution. These diploids are classified as some sixteen subspecies. Nearly all of these have been hybridized and, allowing for some variation in detail, all are inter-fertile (32). The main tetraploid types, subsp glomerata and hispanica, and D. marina all readily form fertile, stable hybrids. Subspecies at the two chromosome levels cross (2n = 14 x 2n = 28) to produce hybrids of two kinds, triploid (2n = 21) and tetraploid (2n = 28), the latter by some form of gametic "non-reduction" (7). Many artificial autotetraploids have been produced, these are fertile but show from 30-50% aneuploidy in F_1 and F_2 progeny (40). Artificial 4x hybrids are stable and fertile. The frequency of quadrivalents at meiosis has given rise to the view that Dactylis is autopolyploid. Interpretation of the naturally occurring tetraploid taxa in terms of the morphological variation present at the diploid level, shows that all such 4x forms are inter-subspecific allopolyploids which may often be of complex origin. Hence, there are very good technical possibilities for using the most diverse gene-sources in the enrichment of breeders material.

Main sources of variation so far utilized include tetraploid populations or diploids (subspecies) predisposed to give large amounts of growth at particular times of the year, and also those with good leaf quality and high digestibility.

The most developed of this material is based on the hybrid between S.37 and artificial 4x subsp. lusitanica, the objective being to improve the winter growth of S.37. One version of this has been produced by directly crossing 4x S.37 and 2x lusitanica pre-selected for winter hardiness. The 4x hybrids were obtained by gametic "non-reduction" without recourse to colchicining, eliminating the artificial autotetraploid

stage from the breeding programme.

4. Intergeneric hybrids between Lolium and Festuca

The phylogenetic proximity of Lolium and Festuca is well established if not well understood, and numerous examples of intergeneric hybrids, both natural and artificial, have been described. While our primary interest in these hybrids is the exploitation of their tremendous potential as breeding material, investigations aim at elucidating the structure of the genera themselves and their inter-relationships. Indeed, these are often prerequisites to the more practical breeding projects.

The development of utilizable varieties from these hybrids has now become a practicable proposition through an increased ability to remove sterility barriers. Through the use of material with artificially doubled chromosome numbers, large families of fertile hybrids can be obtained in several Lolium/Festuca combinations. Breeding projects so far have concentrated on the four intergeneric combinations which can be obtained from Lolium multiflorum, L. perenne, Festuca arundinacea and F. pratensis.

The most thoroughly investigated of these hybrid combinations is an amphiploid (2n = 56) between L. multiflorum (2n = 14) and F. arundinacea (2n = 42) which has shown that desirable attributes from the two species can be combined to give a fertile hybrid with valuable growth features (29). The fertility has been sufficient to produce fairly large quantities of seed, and material from a cross between the varieties S.22 (L. multiflorum) and S.170 (F. arundinacea) has received wide scale testing (Grassld Agron. rep.). However, improvements in establishment vigour, in seed setting capacity and reproductive stability are required before it is considered suitable for release as a cultivar. There is considerable scope for selection within the new and novel variability created by recombination in this cross, and improvement is being sought through selection programmes.

Alternative programmes involve a system of backcrossing the hybrids to diploid and tetraploid forms of L. multiflorum so as to increase the genomic contribution of this parent and thus also improve establishment and early growth characteristics. This backcrossing programme is also aimed at establishing a lower chromosome number in the euploid series, i.e. reducing from 2n = 56 to 2n = 42 and 2n = 28. It remains to be seen whether the frequency of aneuploidy and hence reproductive stability can be better controlled at these lower chromosome numbers (29). Problems of inter-genomic pairing and inter-chromosomal exchange are being coincidentally studied by the Cytology Department.

In addition, amphiploid forms of L. multiflorum (2n = 14) x F. pratensis (2n = 14) and L. perenne (2n = 14) x F. pratensis have been produced which show promising agronomic characteristics. It is hoped that the low chromosome number (2n = 28) of these will prove more stable than the high ploidy forms described above.

Population studies and genetic control of variability

1. Sward dynamics

The grass sward can be seen as a complex and dynamic association of interacting genotypes. Shifts in equilibria follow changes in environmental factors. Studies by A.H. Charles seek to relate changes in equilibria resulting from various management and edaphic forces, to changes in phenotypic expression of the spaced plant. With this information the breeder can attempt to construct a variety which will establish a stable equilibrium under specified management and soil conditions.

Foremost in this programme is a study of survivors from known grassland systems and controlled experiment at successive intervals in time. It is thereby hoped to measure not only the limits but also the rate of change. Competitive and co-operative effects are coincidentally assessed.

First experiments with mixtures of easily identifiable varieties have shown that swards are particularly susceptible to changes induced by management in the period immediately following establishment from seed (8). In consequence of the normal practice of sowing far more seed than can possibly survive, a large decrease in overall population size occurs. This forms a framework within which considerable differentiation can take place. Even in simple mixtures based on cultivars of single grass species rapid changes can occur in response to the environment to which the population is exposed. Older swards composed of a large number of short lived tillers are also capable of quick differentiation in response to agronomic selection pressures (9).

Because of their outbreeding nature single cultivars are themselves mixtures of individual genotypes and some observations indicate that changes can and do occur within single varieties. Changes in morphology are studied with special attention given to the extent to which survival under specific regimes is accompanied by loss (or even gain) in potential production (Plate 1). In one instance of "shift" in a *Lolium perenne* cultivar, the underlying genetic situation is being investigated by M.D. Hayward.

Studies of populations from permanent pastures have also been made. A close relationship between the environment and population structure was again found (10).

In poor edaphic conditions or unfavourable management, selection is for survival in these environments, not for production. This implies that maximum yield can only be achieved if existing populations are replaced. It follows that the full potential of the plant breeders' products can only be realized by close matching of the sward components and the way in which they are used.

2. Population genetics in *Lolium perenne*

Although general genetic principles may derive from fundamental research carried

Plate 1. Differentiation in Lolium perenne L. populations from permanent pastures:- A - Old hay field; B - Fattening pasture

out on laboratory organisms, the genetic architecture of a particular species will depend on its reproductive strategy. This in turn depends on its past evolutionary history and present ecological requirements. Genetic studies in perennial ryegrass are therefore aligned with ecological investigations.

The ecological diversity of this outbreeding species is striking. Early studies by J.P.Cooper and his colleagues established that individuals are highly heterozygous and that rapid response to selection could be obtained for a number of productive characteristics from limited numbers of individuals. It could be inferred that the characters were each controlled by a number of genes with their contributions to the variability being largely additive. Subsequent genetic analyses by means of diallel mating designs have confirmed that gene action is predominantly additive with varying degrees of dominance and little evidence of epistasis (3). This applied to within and between population comparisons including populations from geographically distinct areas of Europe. Indeed, not only is there generally an absence of genetic isolating mechanisms in the species as a whole, but there is no strong evidence of differentiation at the nuclear level into co-adapted gene systems designed to maintain population structure over sexual generations. Genetic homeostasis is thus weak and the species appears to form a single vast reservoir of variability easily exploited by selection.

In a more intensive study of differences between persistent ecotypes from long-established grasslands M.D.Hayward has shown maternally inherited effects which have been interpreted as evidence of plasmon differentiation. Frequently these show as nuclear-plasmon interactions, so that simultaneous selection for complementation between nucleus and plasmon may be inferred (21). A closer study of the vegetative phase of persistent ryegrasses has shown that response to selection for slow and fast rates of tillering (Plate 2) can be evoked during asexual reproduction (6). Responses were genotype dependent and thus suggest a possible way in which co-ordinated genotype/plasmon differentiation could have occurred during the vegetative phase of sward development.

These studies lead to a closer consideration of reproductive strategy in natural perennial ryegrass populations. It can be seen that generation by seed is a colonizing phase, while the development of a population in stable equilibrium with local climatic, edaphic and biotic forces is achieved largely through the vegetative (asexual) propagation of selected genotypes. Unless the habitat markedly changes, sexual reproduction is relatively infrequent, and the species has neither the opportunity nor the requirement of evolving gene inter-relationships (co-adaptation) such as are necessary in shorter-lived species to build up and maintain the adaptive characteristics of the population (ecotype) over sexual generations. The lack of nuclear differentiation and genetic isolating mechanisms throughout the species at large can thus be explained. The exact evolutionary role of the plasmon and its place in plant breeding schemes will require further study.

3. Variety construction and heterosis

The research considered so far has shown that against the highly heterozygous back-

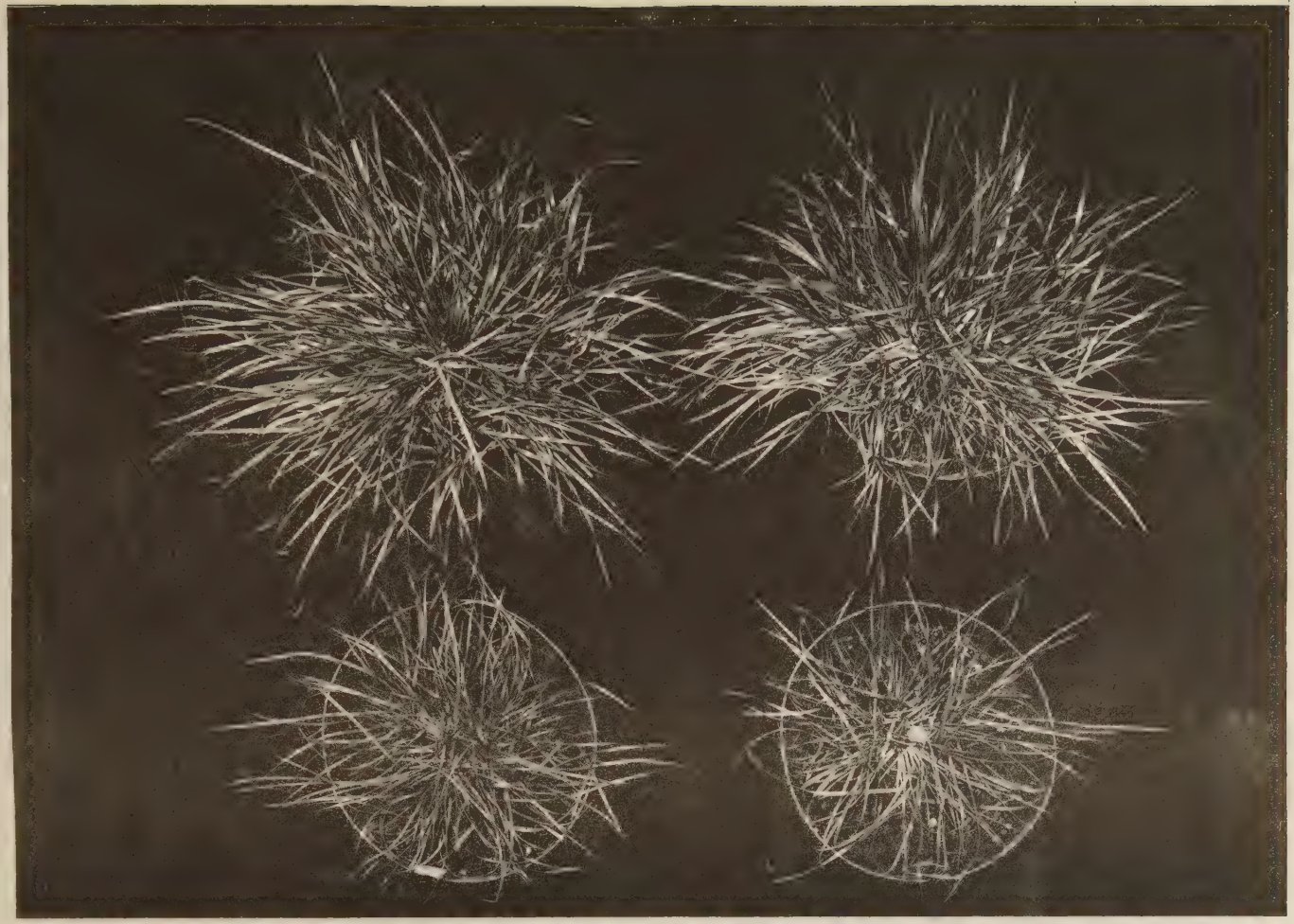


Plate 2. Response to selection for high and low tiller number from within a single genotype of Lolium perenne

ground which is general for the ryegrass species, the effect of a gene substitution is largely additive. Heritability of production characters is consequently high and selection effective, while an adequate level of heterozygosity can be obtained and maintained over 3-4 generations by the synthetic variety.

Inbreeding experiments show that the effects of gene substitutions in more homozygous material are non-additive and heterosis may derive from crosses between inbred lines. Because of the relatively efficient self-incompatibility system operating in ryegrasses, inbred lines are difficult to obtain, and it is doubtful whether F_1 hybrids could be economically produced in this way. Nor would a genetically uniform F_1 necessarily provide the degree of flexibility that variations in practical management demand from present day varieties.

An alternative approach would be to raise the level of heterozygosity above that found in the population at large, or that maintained in synthetic varieties during the 3-4 generations of seed multiplication. C.A.Foster has essayed this by generating seed from binary mixtures of varieties where each member of a pair has similar flowering dates (20). By this means it was hoped to produce commercial quantities of seed, up to 50% of which would be of hybrid origin.

The success of these ventures depends on the extent to which the inter-varietal hybrids demonstrate heterosis for those characters which are important in sward production. The previous studies reviewed earlier have stressed that natural populations of ryegrass do not show marked tendencies towards differentiation with regard to nuclear genes. The survey has, however, not been in detail and it is now being widened to include a greater range of geographic races which can be assumed to have been genetically distinct for long periods of time.

A complementary approach is to obtain genetically distinct populations by artificial selection, and combine these in the hybrid mixtures detailed above. These may be lines selected in parallel for maximum expression of the same character, or the aim may be to combine lines where maximal expression in different characters has been obtained through selection; the latter more nearly representing the 'combination of characters' sought in reproduction of race and species hybrids. These studies should add to our understanding of what constitutes utilizable heterosis when considering the complex requirements for improvement in herbage plants.

4. Genotype - environment interactions

Of all crops, perennial herbage plants have to yield over the greatest diversity of climatic, edaphic and management conditions. As such, the evaluation of interactions of varieties with seasons, locations and management systems poses a major problem. A number of authors have recently adapted regression techniques to the analysis of such interactions, and these have now been applied to herbage grasses.

The technique involves calculating an "environmental index" based upon the mean

performance of all varieties (genotypes) under comparison in each of a set of environments (19). The individual values for each variety are then regressed against the environmental indexes, and the regression value is taken as a measure of the genotypic response to environmental change. Expressed in this way complex genotype-environment interactions have in a number of instances been reduced to differences between linear (response) regressions, and are thus placed on a predictable footing.

Fig.2 illustrates graphically the technique applied to a comparison of herbage from three cocksfoot populations harvested by two different managements (frequent and infrequent cutting) over two seasons and two locations. It can be seen that large interactions (including reversal in the order of performance) between the varieties over the complex of management, climatic and edaphic effects can be adequately explained by differences between linear regressions. Breese (5) has dealt with detailed analysis and interpretation of a similar experiment, and has discussed the limits and uses of these predictive regressions. The use of the technique in measuring change in the level of "dominance" over environments exhibited by a hybrid in relation to the two parental varieties was also considered, and showed that a situation varying from heterosis to intermediate expression may be simply explained in terms of simply inherited linear response regressions.

The techniques are now being used by J.Hill to measure interactions stemming from differential responses to competition between and within species, and in considering factors which affect ryegrass-clover balances in mixed swards.

Already the technique has been successfully applied to a consideration of ryegrass varieties grown over a wide range of locations, under varying managements and over seasons (33). In these studies comparisons were available between the varieties grown as spaced plants and in swards of varying plot sizes. Similar response patterns were distinguished for spaced plant performances and some of the sward reactions, which lends hope that prediction over these density differentials may be possible at least in part.

Grass-clover balance and clover-rhizobial associations

Nitrogen is the key factor in grass production. There are two sources available, fertilizer nitrogen and clover nitrogen. A generous government subsidy of about one third of the cost as well as ease of management have brought about a big increase in fertilizer nitrogen use. Increasing quantities of nitrogen used on grass/clover swards reduce the clover contribution and, at the highest levels, clover may be eliminated completely.

Some farmers believe that clover is beneficial under all circumstances so that anything that can be done to prevent its complete elimination under high N applications would be deemed to be useful. Clover nitrogen is dependent on successful symbiosis with the bacteria *Rhizobium trifolii*. The reactions of rhizobial strains, including ones

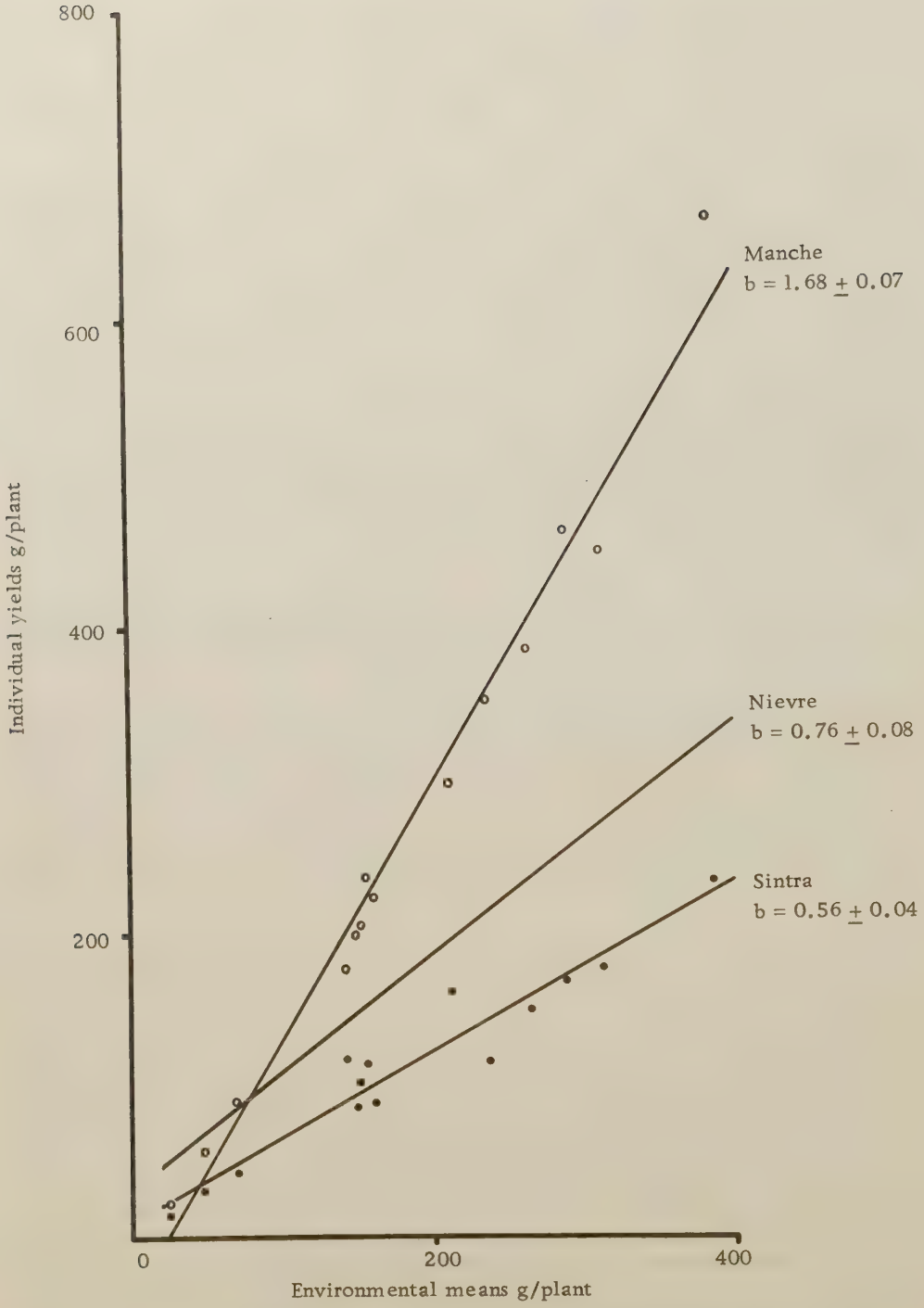


Fig.2. Regression of individual population yields on mean yield for each harvest. Two of the populations with individual points plotted

from high N pastures, to increasing quantities of N in culture have been studied, as well as the interaction of host and bacteria in tube culture tests. Surviving clover plants from high N pastures have likewise been studied and breeding continues of more vigorous, taller growing plants with a longer season of growth (13).

Bacterial strains obtained from high N pastures have been used, but in culture they have given no clear indication of being tolerant to a high N substrate. Neither have survivor plants from high N pastures shown marked adaptation to this environment. Best results have been obtained with medium, large-leaved, tall growing varieties, e.g. Kersey which appear to be able to co-exist with grass under cutting at levels of applied N up to 300 kg/ha. Ecotypes from the Mediterranean region with large leaves and extended growth into the autumn have also been included in the breeding programme (16).

Pure swards of white clover have produced approximately 9000 kg/ha of dry matter containing 335 kg/ha of nitrogen in one year, and this compares very favourably with grass receiving fairly high amounts of fertilizer N.

1. *Rhizobium* variation and clover/rhizobia interactions

The formation of a productive symbiosis between rhizobia and any legume is dependent ultimately on the compatibility of the host and bacterial genotypes. This is evident from the fact that within the *Leguminosae* distinctions can be made between groups of rhizobia because they differ in the range of host species which they can nodulate. For example, rhizobia isolated from the root nodules of *Trifolium repens* are generally able to induce nodulation on most other clover species, but not on legumes outside the genus *Trifolium*. Such rhizobia are said to display cross-inoculation group specificity, and on this basis they have been given specific ranking. At the species level, the nodulation response of individual red clover plants with specific strains of *Rhizobium* has been shown to be critically controlled by the genotype of the host plants (31).

Against this background of interaction between host and *Rhizobium* a research programme was set up to investigate the possibility of producing an improved variety of white clover based on its symbiotic response with *Rhizobium trifolii*. To this end, part of the investigation has been directed at establishing the occurrence of *Rhizobium trifolii*, evaluating the variation within the species and studying the interaction of this species with white clover.

2. Variation in effectiveness of *Rhizobium* isolates

Initially D.G.Jones (24) carried out a bacterial survey with a view to establishing the numbers and variation in effectiveness of *R.trifolii* in soil from a wide range of localities within the U.K. The effectiveness of pure isolates of *Rhizobium* was judged on ability to fix nitrogen, which was itself estimated by the dry matter production of plants of the white clover variety S.100. Inoculated plants were grown in culture

media free of combined nitrogen.

The findings of the survey were broadly that:-

(a) There was a range of variation from ineffective to effective strains;

(b) Strains could conveniently be categorized as effective, intermediate and ineffective;

(c) As the fertility and pH of the soils declined, there was a reduction in overall numbers, and a change in the proportions of each type, the balance moving from predominantly effective strains in the near neutral fertile soils, towards more ineffective types in the less fertile acid soils.

3. Effectiveness in relation to acid production by Rhizobium trifolii

The work of Norris (30) on acid and alkali production by Rhizobium indicates that species of legumes adapted to acid soil conditions are associated with alkali producing rhizobia, whilst legumes adapted to neutral or alkali soils are associated with rhizobia which are acid producers.

There are clear implications of some selective advantage in this situation, probably both to the bacterium in its free existence in the soil, and to the host. This is because, apart from its symbiotic role, Rhizobium is a major rhizosphere organism and may be of importance as such. For example, it may function in neutralizing the root-environment in otherwise extreme conditions of soil acidity or alkalinity. This being the case, the introduction of white clover into an acid soil environment may be greatly facilitated if a symbiotically effective alkali-producing strain of Rhizobium were available to the introduced variety.

To this end a survey of acid production by strains of rhizobia indigenous to soils of varying pH values was carried out by Jones and Burrows (28).

The findings were, broadly that:-

(a) There was a range of variation in acid production by these strains from pH 4.7 to pH 6.95;

(b) There was no relationship between the pH of the soil from which the strain was isolated and the net final pH produced in culture by the isolate;

(c) Effectiveness, as measured in association with S.184 white clover, produced a positive relationship between pH and strains of high effectiveness;

(d) Low final pH in culture was associated with ineffectiveness with the S.184 host.

4. Interaction of host and Rhizobium

From the initial screening of strains for symbiotic effectiveness it was clear that, although the bulk of clover plants in a population of S.100 Nomark would react similarly to a single strain of Rhizobium, there would, nevertheless, be a very wide range of reactions within the population as a whole. The existence of such host/strain inter-

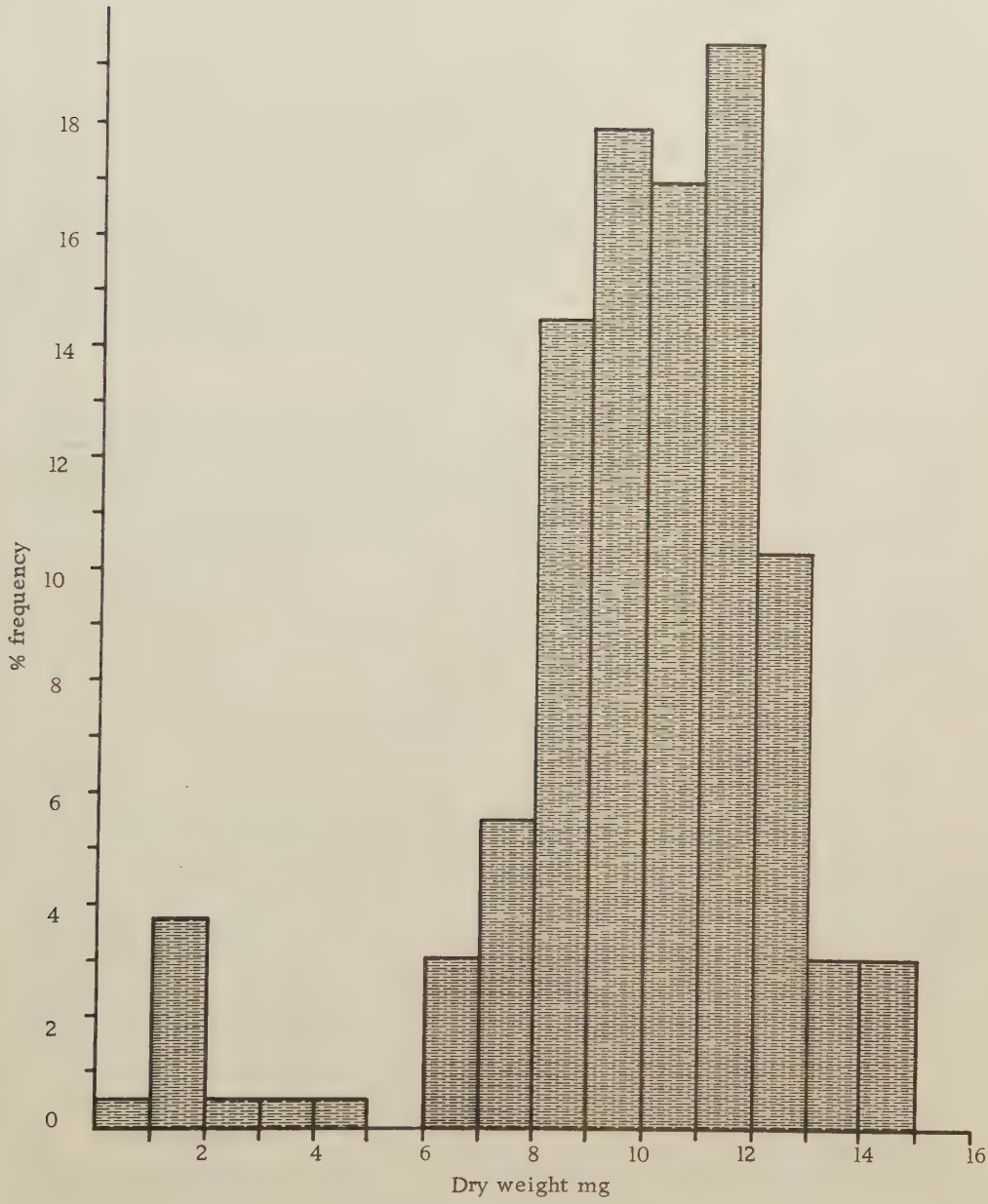


Fig.3. Host plant dry weight after 70 days

actions provides scope for selection. Initially Jones studied the range of such variation in nodulation behaviour within S.100 Nomark white clover inoculated with a known effective strain of Rhizobium. The seedlings showed a range of variation in all the characters studied.

Primary nodulation started 4 days after inoculation, and while the last plants (0.5%) to nodulate did so 12 days later, 50% of the population had nodulated by the seventh day. Earliness of nodulation was negatively correlated with harvest dry weight; thus, rapid nodulation conferred an immediate benefit. The numbers of nodules on the root system at 10 days varied from 2-26, but there was no correlation with final yield. The fresh weight of nodules varied from 2-40 mg/plant, and this was highly correlated with harvest dry weight. The graph of dry weight was a negatively skewed curve (mean 10.1 mg/plant, range 1-15 mg). From these preliminary studies it was clear that earliness of nodulation, and total nodule weight were important factors in determining the yield of these seedlings.

Plants were therefore selected to develop lines with special characteristics, among which were selections for increased nodule tissue. Jones and Burrows (26) demonstrated a significant increase in mean nodule score from 23.3 arbitrary units in unselected S.100 material to 38.9 arbitrary units in the S_1 generation - and a smaller, non-significant increase to 40.0 in the S_2 generation. Increases in nodule volume were accompanied by increases in nodule numbers, and in the S_2 generation there was a positive correlation between mean nodule volume per family and mean family yield. This work is being continued by L.R.Mytton.

Operational breeding

The multi-discipline approach to herbage plant improvement is continually adding to our understanding of what constitutes productive yield (quality and quantity) and what factors limit this in any one of the many environments in which the crop is grown. The breeders' first task is to decide on the priority of the many targets revealed and to judge the feasibility of achieving these from available genetic material. Aims vary from general improvement (e.g. the production of hybrid material with entirely new potentials) to amelioration of specific limitations, such as low digestibility in cocksfoot or disease susceptibility in lucerne. Progress in some current projects illustrating these approaches is discussed below.

1. Ryegrass hybrids

As proposed earlier, an important aim is to combine useful characters from different species. The two ryegrass species Lolium multiflorum and L. perenne are almost fully inter-fertile but stable reproduction of the diploid hybrids tends to break down after the second generation. At the tetraploid level, however, stability in reproduction can be maintained without serious decline over a larger number of generations. The production of commercial quantities of seed from these "permanent hybrids" becomes

therefore an immediate practical proposition, and avoids the necessity for continued F_1 hybrid production with attendant practical difficulties.

D.E.Stephens has now produced large numbers of tetraploid hybrids from selected parents with the intention of introducing higher tillering and a greater degree of perenniality to the otherwise excellent attributes of Italian ryegrass. Winter hardiness of the hybrids has been given a high priority. Promising varieties have been developed and are undergoing agronomic tests. Two of them, carrying Station accession Nos Bb 1237 and 1238, have been registered under the Plant Varieties Rights scheme: they display many of the characteristics of the Italian parent during the establishment and conservation stages, but have better tillering and overwintering properties (see Plate 3).

2. Selection for factors affecting nutritive value (with Chemistry Department)

(i) Digestibility in cocksfoot

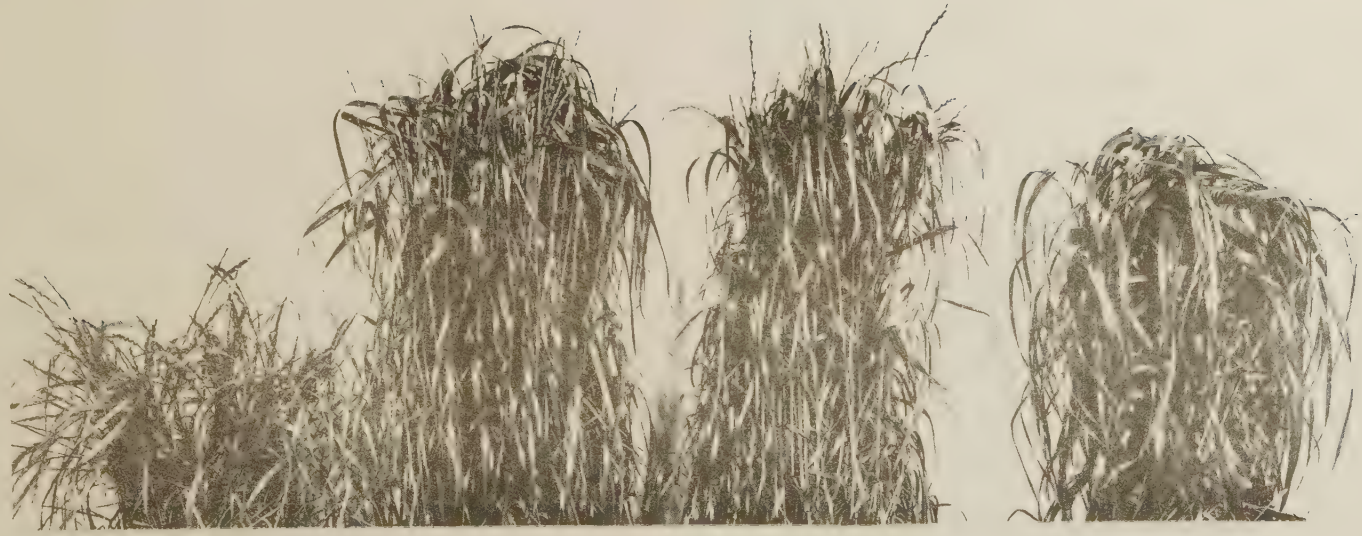
The development of reliable in vitro techniques for measuring digestibility in grasses has led to a large accumulation of measurements for this character for a number of species grown under a wide range of conditions. They have shown that at comparable growth stages cocksfoot has lower values than other commonly used grassland species, and this has been in part held responsible for the decline in usage of this species in grassland farming.

Selection for high and low in vitro dry matter digestibility (DMD) in families deriving from crosses between cocksfoot genotypes was initiated in 1961 by J.P.Cooper to demonstrate heritability for this character. The selection has been continued by Ann C.Thomas in this Department. Altogether three generations of selection have been achieved. The 2nd and 3rd cycles of selection were carried out on spaced plants in the field and each plant was sampled for DMD determination on three occasions in each cycle; during the seeding year, 10 days after head emergence (conservation cut) in the first harvest year, and on one aftermath cut in the same year.

Results for six families involving 3 high selections and 3 low selections, together with a control variety (S.37), are given in Table 1 for the conservation cut during the third cycle of selection. DMD values are the mean of 80 plants.

It will be seen that there has been a strong response to selection in all families. Compared to the control variety (S.37) the response to selection for a high percentage DMD is particularly marked: indeed, these values are well within the ryegrass range at comparable growth stages. It is of particular significance that these high values should be obtained at the "hay" stage (10 days post head emergence) and the material may well cause the role of cocksfoot to be reconsidered in relation to conservation.

It is interesting to note that response to selection is accompanied by marked changes in the physiology and morphology of the plants. The high DMD lines appear to have a faster growth rate, in that the rate of seedling growth as well as the date of heading



L. perenne 4x Hybrid 4x L. multiflorum 4x

Plate 3. Hybrids of perennial ryegrass (Lolium perenne) x Italian ryegrass (L. multiflorum) are sufficiently stable, when made at the tetraploid level, to be maintained over several generations

are considerably advanced over the low selections and the control (see Table 1). On this evidence it might be conjectured that the higher DMD values may be due to a faster rate of cell division and elongation relative to lignification. However, the general morphology of the plant is affected also in that the leaves are longer and possibly tend to be wider (last two columns in Table 1). Most strikingly, the diameters of the flowering stems are greatly increased in some of the high lines (Plate 4), which suggests a difference in anatomical structure.

Table 1. Response in cocksfoot to selection for *in vitro* digestibility (after 3 generations)

Families		Selected character	Correlated responses			
		% DMD (conservation cut)	Seedling* vigour	Mean emergence date (May)	Leaf length cm	Leaf width cm
High selections	1	76.1	10.2	6.4	26.5	0.88
	2	71.3	13.7	12.6	26.3	1.07
	3	69.6	9.3	14.5	30.4	1.33
Low selections	4	59.1	6.5	16.4	22.1	0.80
	5	62.9	5.7	13.0	23.2	0.95
	6	59.5	2.5	20.0	20.0	0.81
Control (S.37)		65.3	6.8	17.8	22.8	0.83

* g dry wt/100 seedlings 6 weeks after sowing

The high lines are now undergoing seed multiplication preparatory to testing the selections for yielding capacity under sward conditions and for feeding value in animal trials.

(ii) Water-soluble carbohydrates (WSC) in ryegrass

Elsewhere in the report it is argued that a significant measure of food value in the herbage grasses is the amount that the animal will consume over a specified period of time (intake). In the ryegrasses digestibility is generally so high under good management systems that it is not a significantly limiting factor of intake. Evidence has been produced to show that other biochemical constituents may affect the level of intake, particularly the protein/carbohydrate balance and mineral contents. Vose and Breese (34) have shown that the level of protein and water-soluble carbohydrate (WSC) fractions of the plant are heritable traits showing partial negative correlation. Moreover, there were large differences between genotypes within a variety. It was decided, therefore, to select lines of perennial ryegrass which contrasted in the proportions of these classes of biochemical constituents, so that a critical evaluation of differing protein/carbohydrate balances under different management systems could be attempted

Plate 4. Selection for high and low *in vitro* dry matter digestibility in cocksfoot (*Dactylis glomerata*) for three generations.
Left - low selection line; Right - high selection line

Note: The leaves are longer and wider in the 'high' line and the diameter of the stems is greatly increased.

in conjunction with animal trials.

Selection was primarily for high and low percentages of WSC and was initiated within a single ryegrass variety (S.23). Assessment was on spaced plants grown in the field which were cut frequently throughout the season. Four cuts were sampled over two years for each cycle and the mean values provided the selection criteria. Three high and three low families were initiated and a system of cyclic mating among families within selection lines was adopted for selected genotypes so as to avoid inbreeding.

Results presented in Table 2 show that selection has been effective by the third cycle. There have, however, been disadvantageous correlated responses. Thus, susceptibility to rust infection (Puccinia coronata) has markedly increased in the high lines (see Table 2). The increased susceptibility of grass species with high levels of WSC to certain classes of fungal pathogens has previously been reported by Carr (Plant Pathology report). In the present instance, however, there is still marked variation in susceptibility among the high lines so that it may be possible to coincidentally select for high WSC and high resistance.

A further correlated response was a decrease in seed fertility in the high lines, though not in the low. These selections will now undergo seed multiplication for wider scale assessment.

Table 2. Response in perennial ryegrass to selection for high and low percentages of WSC - after 3 generations

Families		Selected character % WSC**	Correlated response Susceptibility to rust*
High selections	1	19.8	3.6
	2	20.5	2.7
	3	20.5	1.7
Low selections	4	14.9	0.3
	5	14.8	1.9
	6	15.3	1.3

* Eye estimate of degree of infection, 0 = resistant to 5 = most susceptible

** Mean plant value averaged over 4 cuts (number of spaced plants per family varies from 27-80)

3. Breeding for resistance to Verticillium wilt disease

Lucerne is a crop with a potential which has not often been achieved for several technical reasons. In recent years it has suffered a further set-back because existing varieties are susceptible to the fungus disease Verticillium albo-atrum. This disease

is now widespread in lucerne growing areas and is the main cause of the reduction in the economic life of lucerne leys. As a result, the acreage has tumbled from over 100,000 to slightly less than 40,000.

Earlier studies suggested that all cultivated varieties were highly susceptible to the disease and this tended to deter a search for resistance within them. Instead, workers looked at other related wild species where a degree of resistance was found. Unfortunately these wild species were agronomically poor types so that a long programme of back-crossing would be necessary before anything worthwhile could be produced.

However, further observations on old stands which had become naturally infected with Verticillium showed that some plants appeared to remain in a healthy condition over a period of five years. Selections from this source were chain crossed and the progeny established in a disease nursery. Before transplanting, the roots were dipped in a suspension of Verticillium inoculum, and 20-30 dead wheat grains on which the disease was growing were placed in the dibble hole. As a result, the disease developed uniformly over the area and symptoms became visible within six weeks of planting in August.

The percentage of dead plants in June of the following year is shown in Fig.4. Crosses had been made within three maturity types, early, mid season, and late, and seven control varieties were included. The control variety du Puits and AF1, a derivative of late lucerne, proved to be very susceptible, 80% of the plants being dead at this date. The mortality in remaining control varieties ranged between 51-73%, the variety showing the lowest figure was a wilt resistant selection from Italy.

Most of the progenies within all three maturity types showed superior survival. It was clear from these results that some families showed exceptionally high degrees of resistance to Verticillium wilt disease (Plate 5).

Selfed progenies of these same plants were also available in these tests. In general, the effect of inbreeding was to reduce vigour, and poorer values for yield survival and wilt scores were obtained.

Further selections from this material have been continued and a multiplication of a potential variety AF7 has taken place.

4. Storage of clover seed

Successful seed storage is the most economical method of conserving plant material for future use. This material may be required in order to preserve genetic variation of value to the breeder or genetic uniformity for maintaining established cultivars. Conditions are required which prolong the life of the seed while reducing to a minimum any genetic change in the material.

Red clover seed stored in an open tube at room temperature, deteriorated rapidly

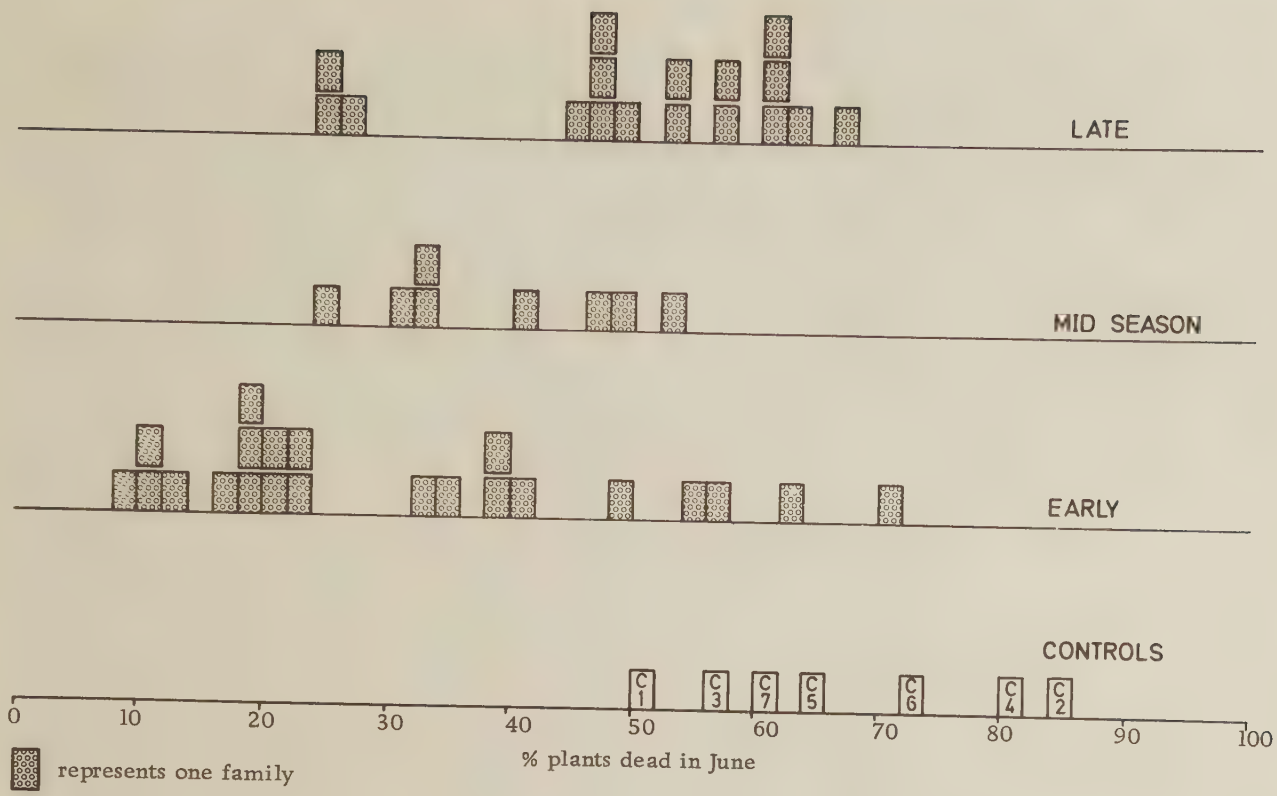


Fig. 4. Percentage of dead plants in families from which lines resistant to Verticillium wilt were selected (mean family size = 82 plants)

Plate 5. The three families on the left show excellent survival after artificial infection with Verticillium wilt disease. Families to the right show poor survival and include one control variety Provence.

Note: Each row (= family) originally established with 25 plants.

after 3-4 years, but when the tube was sealed its longevity was doubled (12). Storing the seed at 0°C extended viability to at least 15 years before a gradual decline set in. White clover in sealed tubes at room temperature maintained its viability for about 15 years compared with 4-5 years in an unsealed tube. At 0°C, however, white clover maintained high germination under each of four different gaseous environments over a period of 21 years.

After 16 years a check was made to see if these storage conditions had affected plant phenotype, but one problem is the difficulty of obtaining an adequate control for such an experiment. The controls used were later generations of the same stock, although this introduces two sources of variation unconnected with storage: (a) the possibility of shift during multiplication, and (b) the environmental conditions when the respective seed lots were produced and which could have a profound effect on subsequent performance.

Bearing in mind these limitations, N.R.Young found that seedling vigour was lower in stored seed, especially where the treatments had resulted in a low germination capacity. Recently harvested seed had a slight advantage in several vegetative characters of spaced white clover plants and in yield of both species. In refrigerated seed of white clover, stored in vacuum, and in nitrogen, a slight lowering of pollen fertility and seed setting ability was detected when compared with sealed and open tube storage.

Progenies derived from the stored seed of white clover were also examined, but no inherited reduction in seed setting ability was found.

5. Variety production in relation to agricultural requirements

The potential of many existing varieties is still far from being fully exploited under most farm systems, while demand for some of the better varieties often exceeds supply. To avoid further complication of this already complex situation, it has not been the policy of the Station to add to the wide range of marketed varieties unless a particular deficiency in the range can be specified, or significantly new and different potentials may be offered (as for instance through the production of novel hybrids). As discussed, in all instances it has been the aim of the Station to first adequately test the material under appropriate farm systems. The contribution of S varieties to the present day agriculture is summarized below.

Altogether 21 varieties of grasses and clovers have been released to the trade, fourteen in the 1930s, two in the 1940s, two in the 1950s and another three in the 1960s. Not all these grass varieties are for strictly agricultural use, S.59 red fescue and S.50 timothy being used mainly as amenity grasses. Of the agricultural varieties all but one continue to be recommended by the National Institute of Agricultural Botany. It can be seen therefore that some varieties have now been in the market for more than thirty years and their use is still increasing, e.g. S.24 perennial ryegrass.

The following list includes all varieties that have been released to date:

Perennial ryegrass	S.23, S.24, S.101, S.321
Italian ryegrass	S.22
Cocksfoot	S.26, S.37, S.143, S.345
Timothy	S.48, S.50, S.51, S.352
Meadow fescue	S.53, S.215
Tall fescue	S.170
Red fescue	S.59
Red clover	S.123, S.151
White clover	S.100, S.184

Descriptions of these varieties have appeared in many of the Station's publications and in Farmers' Leaflets published by N.I.A.B.

Changes in farm systems may, however, reveal deficiencies in the existing range. Thus, apart from the projects previously discussed, breeding programmes have been initiated to develop perennial ryegrass varieties with an increased response to high N levels, which will withstand high stock densities and have an improved resistance to winter kill. Improved yield under high N application, coupled with a high degree of winter hardiness, is also receiving attention in Italian ryegrass. Breeding projects in white clover include these with the intention of improving ability to yield well in mixtures with grasses grown under high N levels.

A new medium-large-leaved white clover AC1, bred from seed collected in Normandy, is being multiplied for release. It has proved higher yielding than S.100 (14), more persistent and more aggressive in grass/clover mixtures, especially in the presence of fertilizer nitrogen (Plate 6).

In red clover, a new early broad red type AA14, bred from a Glamorgan stock, will soon be available. It combines a higher degree of persistence with considerable resistance to clover eelworm. First year yields are similar to Essex Broad Red, but in the second and third years it is considerably superior. Its flexibility under different management contingencies has been favourably commented on by the agronomists.

FUTURE PROGRAMMES

Throughout this report the need for clearly defined agronomic objectives as a prerequisite to breeding operations has been emphasized. For herbage crops these objectives have to be defined within the context of animal feeding systems with worthwhile economic returns. The requirements are, therefore, complex and have to be translated into physiological and biochemical criteria which can be assessed at the individual plant level. It is thus apparent that herbage crop improvement must involve a comprehensive research programme and that significant advances can only emerge from a closely co-ordinated multi-discipline approach.

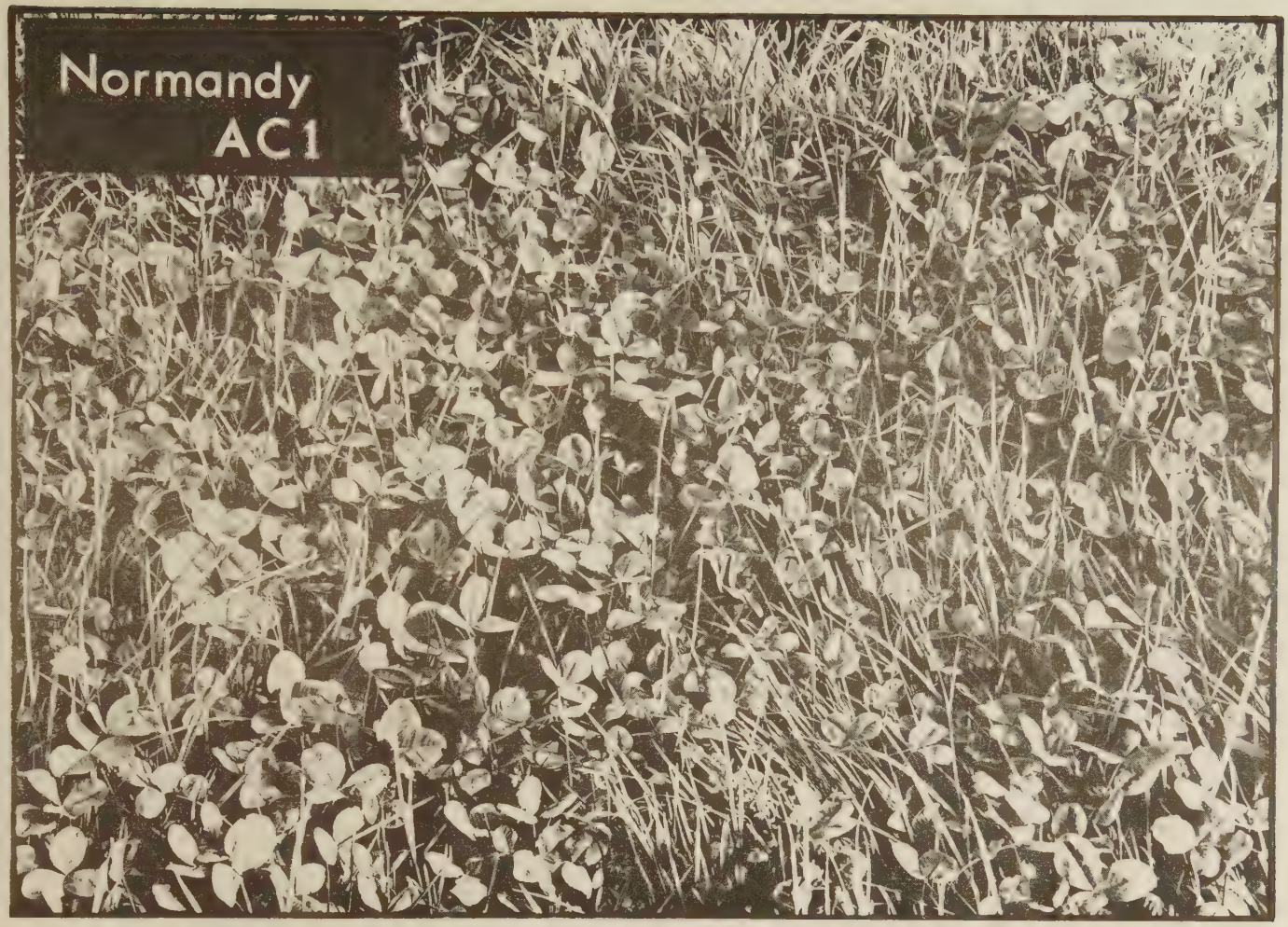


Plate 6. A close-up of a plot sown with S.24 perennial ryegrass and AC1 white clover.
Note: vigorous growth of medium large-leaved clover.

Once variety models have been appropriately described, progress in breeding depends on two factors, the discovery of new materials and the development of new breeding methods.

Until recently a wealth of naturally occurring genetic variability in herbage species was to be found in natural grasslands and uncultivated wastelands in Britain. Collection has given rise to a large range of edaphic and biotic adaptations (ecotypes) which have been supplemented by climatic variants through introduction from other countries. With the advance of modern agriculture (and increasing urbanization) natural habitats are becoming scarcer and primitive cultivars are being replaced by improved varieties. The future will see an increasing need, therefore, for conserving these most valuable and diminishing genetic resources. This raises problems of the way in which this might be accomplished - by attempts at in situ preservation, or by collection and propagation through seed, coupled with long term seed storage.

Bearing these points in mind the Plant Collection and Introduction Unit of the Department will continue the systematic collection and screening of material from an extended range of climates and ecological habitats and, within the limits of the resources, will endeavour to produce and maintain seed stocks of the more valuable material. It is hoped that an effective liaison with F.A.O. (or other international organization) may be forged so that standardized collecting and evaluating procedures are adopted, and a centralized system of collation, recording and dissemination of descriptive data evolved. In this way the Station could serve as a major centre for the international exchange of herbage crop collections and so facilitate the availability of valuable genetic resources.

Many of the valuable characteristics obtained through the plant introduction programmes are contained in distinct geographic races or species which frequently fail to form fertile hybrids with types in agronomic use. This is particularly so for Festuca and Dactylis spp. The incorporation of these characteristics into existing varieties involves the manipulation of chromosomes and chromosome sets by sophisticated hybridization techniques, including colchicine treatment and embryo culture. The aim in this direction must be towards greater precision in controlling genetic exchange through a better understanding of species and race relationships and chromosome affinities. Cytogenetic studies have already provided the means to obtain varying genomic combinations between Lolium and Festuca. They lend hope that further studies on these two genera may open new avenues for the direct and indirect exchange of genetic material, to the generation of new species, and so to the construction of a range of entirely novel plant types. In this way we can hope to break the physiological barriers imposed by natural selection on the parents, and provide fresh starting material which is malleable enough to be more specifically moulded to the needs of the grassland crop. Although the greatest potentials at the moment appear to be offered by the Lolium/Festuca complex of species, other genera, notably Dactylis, are also under investigation.

Although interspecific hybridization may provide a major innovation in obtaining

advanced material, the studies considered earlier in this report point to the large reservoirs of variability maintained in the heterozygous individuals of the species by the outbreeding mechanisms. It has been demonstrated in ryegrass and cocksfoot that large responses can be obtained to selection within populations or in crosses between populations. This is particularly so for the diploid ryegrasses, and selection for required physiological or biochemical expression should be effective. Studies are now under way to determine what limits are set to these responses by undesirable correlated responses in other characters. Genetic analysis will determine whether these correlations can easily be broken, and the extent to which F_1 hybrids may be successful in generating enhanced expression over a number of characters.

The scope for rapid selection under the competitive conditions of the sward has been noted. This raises possibilities for establishing techniques whereby large numbers of genotypes can be exposed for mass selection under specialized managements. This approach is currently being tried where selection criteria cannot yet easily be defined. Examples are in the selection of populations suitable for use in grassland systems with high nitrogen input and high stock densities, in selecting genotypes suitable for hill environments, and in selecting plants resistant to winter kill. Survivors not only form useful collections of adapted material, but also provide information on the criteria which predispose adaptation.

Adaptation to a particular set of conditions depends not only on the genetic variability available for selection, but also on the plasticity exhibited by individual genotypes. Clearly, a better measurement of genotype/environment interactions will add to our understanding of differing adaptabilities among genotypes. We have seen that regression technique can provide predictive measurements of response to changing environmental conditions and thus afford an assessment of the flexibility in genotypes and varieties with regard to utilization over locations and under differing managements. As such, they could be used to specify the range of managements which may be tolerated.

It has also been seen that adaptation in persistent ryegrass genotypes may be predisposed by extra-nuclear variability in the plasmon. Too little is yet known about this extra dimension of variability to predict how this may best be exploited at the breeding level, but directed selection for increased growth rate during vegetative propagation is an intriguing possibility. Whether differences artificially induced in this way can be transmitted over sexual generations has still to be established.

So far grass crops have not been grown intensively enough to run risks of disease attacks of epidemic proportions. Disease risks will, no doubt, increase as grass utilization intensifies. In these perennial crops, virus diseases are likely to be especially important and there are already reports of increasing virus infections. The role and nature of many viruses have still to be elucidated, particularly in relation to their effects on yield and persistency. Clearly, plasmon constituents which can be altered by selection and infective cell inclusions will have to be studied conjointly, and genetic studies in the more perennial grasses will have to involve a close consideration of the relationship between the nucleus and these extra-nuclear components.

The nutritive value of the herbage legumes is now well established, while under more extensive farm systems the nitrifying property of associated rhizobia is likely to be an economic source of plant nitrogen during the foreseeable future. Efficient symbiosis will therefore be a valuable feature of clover crops grown under these conditions and merits continued research on both Rhizobium and legume. For more intensive systems further research is required into the feasibility of growing mixtures of grass and clover, or of growing and harvesting them separately, followed by mixing before feeding. Under the latter system, and particularly where conservation is intended, lucerne or other legume species may prove an advantage.

Measured on the evolutionary time scale of most cultivated species, herbage plants have a very short history of intensive cultivation as farm crops. During fifty years of conscious plant breeding, signal advances have been made in accumulated knowledge of the crop species and in the production of outstandingly successful varieties. Still we see that the wealth of genetic variability is largely untapped. The case has been made that the effective harnessing of these resources will depend first on a proper description of variety models in physiological and biochemical terms, coupled with a full appreciation of genetic control. The genetic tailoring to meet requirements will in turn depend on an effective application of modern technology to screening and selection processes, and the use of computer facilities in the storage, retrieval and processing of information data.

References

(1) M. Borrill, F. Gonzalez-Bernaldez and Ruth Lindner, (in press), Boletin Real Soc. Espanola Hist. Nat.

(2) M. Borrill, B. F. Tyler and M. Lloyd-Jones, (in press), Cytologia.

(3) E. L. Breese, 1960, Proc. VII Int. Grassld Congr. Reading, 45-49.

(4) E. L. Breese, 1966, In: Reproductive Biology and Taxonomy of Vascular Plants. Rep. Conf. Bot. Soc. of Br. Isles. Ed. J. G. Hawkes, Pergamon Press, 51-60.

(5) E. L. Breese, 1969, Heredity, Lond. 24, 27-44.

(6) E. L. Breese, M. D. Hayward and A. C. Thomas, 1965, Heredity, Lond. 20, 367-379.

(7) C. P. Carroll and M. Borrill, 1965, Genetica 36, 65-82.

(8) A. H. Charles, 1961, J. Br. Grassld Soc. 16, 69-75.

(9) A. H. Charles, 1964, J. Br. Grassld Soc. 19, 198-204.

(10) A. H. Charles and C. B. Crampton, 1963, In: Soil Moisture. Welsh Soils Disc. Group Rep. No. 4, 89-96.

(11) H. Daday, 1958, Heredity, Lond. 12, 169-184.

(12) W. Ellis Davies, 1965, J. Br. Grassld Soc. 20, 180-181.

(13) W. Ellis Davies, 1969, In: Grass and Forage Breeding. Occ. Symp. No. 5, Br. Grassld Soc. 21-27.

(14) W. Ellis Davies, 1969, J. agric. Sci., Camb. 73, 139-144.

(15) W. Ellis Davies, 1970, In: White Clover Research. Occ. Symp. No. 6, Br. Grassld Soc.

(16) W.Ellis Davies and Norman R.Young, 1967, Euphytica 16, 330-340.
(17) Alice M.Evans, 1955, New Phytol. 54, 149-162.
(18) Alice M.Evans, 1962, Euphytica 11, 164-176.
(19) K.W.Finlay and G.N.Wilkinson, 1963, Aust.J.agric.Res. 14, 742-754.
(20) C.A.Foster, 1968, Intervarietal heterosis in Lolium perenne L. Ph.D. Thesis, The Queen's University of Belfast (unpublished).
(21) M.D.Hayward and E.L.Breese, 1968, Heredity, Lond. 23, 357-368.
(22) T.J.Jenkin, 1955, J.Genet. 53, 467-486.
(23) T. J. Jenkin, R. G. Stapledon and R.D.Williams, 1931, In: Bull.No.3, Imp. Bur.Pl.Gen.Herb.Plants. The Breeding of Herbage Plants: Technique adopted at the Welsh Plant Breeding Station, 1-77.
(24) D.Gareth Jones, 1963, J.Sci.Fd Agric. 14, 740-743.
(25) D.Gareth Jones and Angela C.Burrows, 1969, Soil Biol.Biochem. 1, 57-61.
(26) D.Gareth Jones and Angela C.Burrows, 1968. J. agric. Sci., Camb. 71, 73-79.
(27) E.T.Jones, 1955, A review of the early work of the Welsh Plant Breeding Station, 1-15.
(28) Alec Lazenby, 1957, J.agric.Sci., Camb. 48, 294-304.
(29) E.J.Lewis, 1966, Proc.Xth Int.Grassld Congr., Helsinki, 688-693.
(30) D.O.Norris, 1965, Pl.Soil 22, 143-166.
(31) P.S.Nutman, 1954, Heredity, Lond. 8, 35.
(32) P.F.Parker and M.Borrill, 1968, New Phytol. 67, 649-662.
(33) C. J. A. Samuel, J. Hill, E. L. Breese and Alison Davies, (in press), J.agric. Sci., Camb.
(34) P.B.Vose and E.L.Breese, 1964, Ann.Bot.N.S. 28, 251-270.
(35) R.D.Williams and W.Williams, 1947, J.Genet. 48, 69-79.
(36) 1958 Welsh Pl.Breed.Stn Report for 1950-1956, 11-35.
(37) 1963 Welsh Pl.Breed.Stn Report for 1962, 26-27.
(38) 1965 Welsh Pl.Breed.Stn Report for 1964, 35-36.
(39) 1966 Welsh Pl.Breed.Stn Report for 1965, p.30.
(40) 1967 Welsh Pl.Breed.Stn Report for 1966, 48-56.

GRASSLAND AGRONOMY

ROY HUGHES

THE EARLY YEARS, 1919-1939

The history of the Agronomy Department in the early years of the Station can be followed very largely through publications. The Station Series H bulletins formed the principal means of presenting the results of agronomic research, and the first of these, "Preliminary Investigations with Herbage Plants", published just three years after the Station's foundation is a monument to the industry of the members of staff. The investigations reported dealt primarily with the yield throughout the season from plants originating from seed obtained from a wide range of sources. Such data were an essential prerequisite to the breeding programme which aimed at producing "strains" suitable for temporary leys. It is of interest that this early agronomic work was carried out by Sir George Stapledon with two men who were later to become famous as plant breeders - T.J.Jenkin and R.D.Williams.

The next series of papers on agronomic topics appeared two years later in Bulletin Series H No.3 (1924) which was much more ambitious in scope, and the first major publication to proclaim the value of indigenous as compared to commercial strains. Two other significant developments were reported in the Bulletin. The first was the use by Professor Fagan of chemical analysis to assess the nutritive value of the herbage. The other was contained in the paper entitled "Grassland and the grazing animal", which was of major significance since it presented the concept that the grazing animal was not just a defoliating machine, and inaugurated the movement of the agronomic work away from a purely botanical outlook. In the following year a paper on the "Relative palatability of pasture plants" appeared in the Journal of the Ministry of Agriculture, Fisheries and Food (6) published by William Davies, the first head of the Grassland Agronomy Department and a future director of the Grassland Research Institute, Hurley. It revealed that in the mid-twenties there was already a clear appreciation of the fact that the value of a herbage plant largely rested upon how much of it an animal would consume. Studies on chemical composition and palatability emphasized the value of young grass and of the leaf fraction, the basis of modern grassland management.

The importance of the animal in grassland studies and of extending the grazing season was further emphasized in the H Bulletin No.5 (1927), "The Animal Complex and the Pasture Complex" which contained two papers. The first, a joint investigation by the agronomists and chemists, was on Italian ryegrass for winter and early spring keep,

a continuation of earlier work that emphasized the winter greenness of this species. The investigation is noteworthy for its emphasis on sheep grazing as the means of defoliation and for showing conclusively that the sheep preferred leaf to stem. Out-of-season grazing was a topic which intrigued both Stapledon and Davies and a considerable effort has been continually devoted to its improvement by breeding and management. The second paper was by Stapledon and Martin Jones on the sheep as a grazing animal and as an instrument for estimating the productivity of pastures. The amount of herbage actually eaten by sheep was measured, selectivity of grazing assessed, and details were given of the time spent by sheep in grazing, chewing, lying down and standing up. This was one of the first reports on the behaviour of grazing animals since James Anderson published his observations in 1790. Behaviour of the grazing animal continued to be studied up to 1939.

The above techniques were later used by Martin Jones for comparing the relative performances of temporary and permanent pastures (10). Both the response to nitrogenous fertilizer and the liveweight gain of sheep were found to be greater on the temporary ley. It was also found that the time spent by an animal chewing the cud and resting on a particular pasture gave a useful indication of its nutritive value:- the more time spent resting, the better the pasture.

These techniques were developed further to study the effect of the length of the period of rest in rotational grazing. It became clear that botanical composition of a sward could be influenced by grazing treatment. These studies were subsequently extended by Martin Jones (at Jealots Hill) and by Ll.I.Jones at Aberystwyth whose investigation involved a study of eleven seeds mixtures and ten managements (9). The effect of management upon the type of plant which survived within a species was also studied.

In addition to the effect of grazing on botanical composition, the effect of the return of dung and urine upon the yield of the sward was also studied. This highlighted the fact that much more dunging and urinating occurs at night, resulting in the depletion of fertility from a pasture grazed only by day and a build up of fertility in one grazed only at night.

Simultaneously, investigations were being carried out on problems of seeds mixtures. Two H Bulletins No.6 (1927) and No.8 (1928) were entirely devoted to this topic. The papers in the former dealt with germination and establishment of different species and strains with reference to environmental factors both in small scale and field trials. The conclusion derived from these trials summarized what was later to become the theme of Stapledon's thinking on seeds mixtures "to reduce the numbers of species and to sow the appropriate species heavily - and so to arrange the mixture as to give the species which have the best chance of becoming the ultimate dominants the earliest possible opportunity of assuming their legitimate position".

Bulletin No.8 contains results of some complex experiments presented in terms of yield and persistency of the constituents of the sward. An interesting conclusion re-

flecting the current value of herbage varieties was that "except on fields of unusually high fertility, or perhaps under continuous heavy manuring, the only species (when represented by the ordinary seed of commerce) which can be regarded as usefully persistent subsequent to the fourth harvest year are rough stalked meadow grass, crested dogstail and wild white clover. There are indications now that to this list will probably have to be added good strains of wild red clover and improved indigenous strains of perennial ryegrass, cocksfoot and perhaps timothy..."

Stapledon considered the Cockle Park type mixture to be out of date, but since its use would undoubtedly continue, he suggested how it might be improved. His version is given below.

Basal mixtures VI

Perennial rye-grass:	
Ordinary commercial	7 lb
Indigenous ex Kentish pastures	
or	7 lb
Station S.23	
Cocksfoot:	
Ordinary Danish	2 lb
Akaroa	3 lb
Station S.26	3 lb
Timothy	4 lb
Rough-stalked meadow grass	
and/or	
Crested dogstail	3 lb
and/or	
Red fescue	
Late-flowering red clover	4-6 lb
White clover	0.5-1 lb
New Zealand certified	0.5-1 lb

An important study dealt with the aggressiveness of one species towards another when sown together. This paper was to have a great influence on later thinking, as species were grouped according to their aggressiveness and it was possible to show the wastefulness of sowing a non-aggressor species with an aggressor. Finally, Stapledon and Davies summed up their views and suggested simpler seeds mixtures, still complex by present day standards, containing up to nine species, but emphasis was laid upon "informed blending of strains of the same species". Stapledon still hoped to achieve the best of all worlds in one sward, both early and late growth, together with the maximum mid-season production. It was not until the mid- and late 1930s that papers

stating the value of the simple seeds mixture, for which the Station became noted, were published. This realization occurred with the introduction of the Station bred varieties and of the concepts developed in association with their seed production.

One feature of these seeds mixture experiments was the use made of experiments carried out on farms under the control of the farmer. Stapledon had established such experiments soon after he arrived at Aberystwyth and during the period 1929-1933 no less than 848 acres on 231 different farms in Wales were sown out to plots and experiments. Many of the leading pioneers of farming collaborated in this work, e.g. Stanley Bligh of Cilmery, Builth Wells, and Bennett-Evans of Manod, Llangurig. By 1937 there were 250 trials in Wales and also 22 trials in England conducted as the result of a grant received from the Royal Agricultural Society of England to extend into England the work being carried out in Wales. Although only limited data could be collected from these trials, nevertheless they had the advantage that new seeds mixtures and new varieties could be tested under actual farm conditions and under such varied environments which could not be simulated at a research station.

The use of nitrogenous fertilizer on leys was another subject closely studied. As early as 1926, Stapledon and Beddows had reported in some detail on the effect of nitrate of soda on the growth of cocksfoot, taking into account the effects upon tiller number and root growth as well as on yield. Bull.H No.9 (1928) dealt with the effect of nitrate of soda on a simple Italian ryegrass, perennial ryegrass and white clover ley. By present day standards the amount of nitrogen applied was low (70 kg/ha/year). This investigation showed an increase in yield and an extension of the growing season due to nitrogen as well as a depressing effect upon the clover when grasses were allowed to overshadow it.

Other experiments highlighted the interaction between nitrogenous fertilizers and clover, with considerable increases in yield being obtained from the swards of grass alone, but little increase from those containing a high proportion of clover. As white clover had shown itself to be of excellent nutritive value for sheep and capable, with grass, of producing yields comparable with those produced by the levels of nitrogenous fertilizer then in use, Stapledon remained unconvinced of any great value in nitrogenous fertilizer.

Manurial trials were not limited to those dealing specifically with nitrogen. A series of plots were laid out on contrasting pasture types, from poor Molinia upland to good temporary leys in the lowland, treated with combinations of NPK. It was shown that an increase in soil fertility tended to increase the contribution of the better grass species. The most dramatic responses were seen in the hills and uplands.

In 1931 the first varieties of grasses bred by the Station were released to the seed trade, and in the following years Stapledon with W.E.J.Milton reported on comparisons of these with commercial varieties. In these experiments sheep were widely used for the evaluation of varieties on a large scale, and the results showed the superiority of pedigree varieties not only in yield, but in many other important attributes, partic-

ularly leaf to stem ratio and winter growth. Possibly the only criteria in which the pedigree varieties did not show up well was in the yield of hay. Nitrogenous fertilizer tended to level out the differences between the strains in respect of yield. Having asserted that no two strains react in precisely the same way to any factor that influences any property of a sward which affects its economic value, Stapledon suggested that the only way to manage grassland properly lay "in a simplification of the botanical personnel of our swards". Following this statement Stapledon, once again, emphasized the need for an "enormous amount" of critical field experiments before scientific rules for grassland management could be formulated.

The year 1933 marked the end of an outstanding decade in grassland research. That this year was a milestone in Stapledon's mind is shown by his production of An Account of the Organization and Work of the Station from its Foundation in April 1919 to July 1933 which explained the aims of the Station and discussed at considerable length the results obtained at the Station up to 1933. By this date, eight grass varieties had been released to the seed trade and the seed of another thirteen was being multiplied prior to release. While much remained to be done before he could recommend a "scientific method of grassland management", much had been learnt about the behaviour of swards and their economic value. Many of the problems of establishment had been resolved following detailed work into depth of sowing, seed quality and seeds mixtures. The new varieties provided the basis from which worth-while swards could be produced, and the improvements being sought in methods of seed production enabled seed of these varieties to be marketed at reasonable prices. Even today Stapledon's summary of the work remains a text-book to which little has been added except detail, while his list of rules and axioms for the grazier are uncannily appropriate to current intensive grazing systems.

After 1933 few entirely new ventures were started, and the emphasis changed from the general agronomy of varieties and species to comparisons of the newly released Station S varieties with those commercially available. More attention was paid to specific problems such as winter keep and hill improvement, as opposed to more general agronomy of species.

EARLY HILL LAND INVESTIGATION

Soon after his arrival in Aberystwyth in 1912 Stapledon made a vegetation survey of a large part of north Cardiganshire, which was to have important consequences. An ecological survey such as this he was later to describe as "the best of all possible and sensible beginnings" for investigations into the improvement of hill land. From the survey arose not only the work on hill improvement, but also the conviction that a survey was the best beginning to grassland improvement as a whole. This in turn led to the grassland survey of England and Wales, although this was not to be completed until 1940.

Almost from the foundation of the Station, Stapledon laid down plots on hill farms and took every opportunity to campaign for more facilities for experimental work on

the hills. Most of the farm trials studied the effect of manures upon natural swards; some of these experiments were carried on into the 1950s, being the subject of a number of papers by W.E.J.Milton (12). Other experiments concerned reseeding and evaluation of seeds mixtures. The early work showed the value of rape as a pioneer crop, and of wild white clover in the resulting sward; Stapledon was quick to point out and utilize a cheap source of wild white clover seed, viz. seed cleanings.

The influence of an abundant stand of wild white clover on the nitrogen and lime content of herbage is well illustrated by the figures below.

	% in dry matter	
	N	Lime
A No treatment	1.79	0.398
B Complete manures + lime and cultivation	2.23	0.622
C As 'B' plus seeds including wild white clover	2.47	1.384

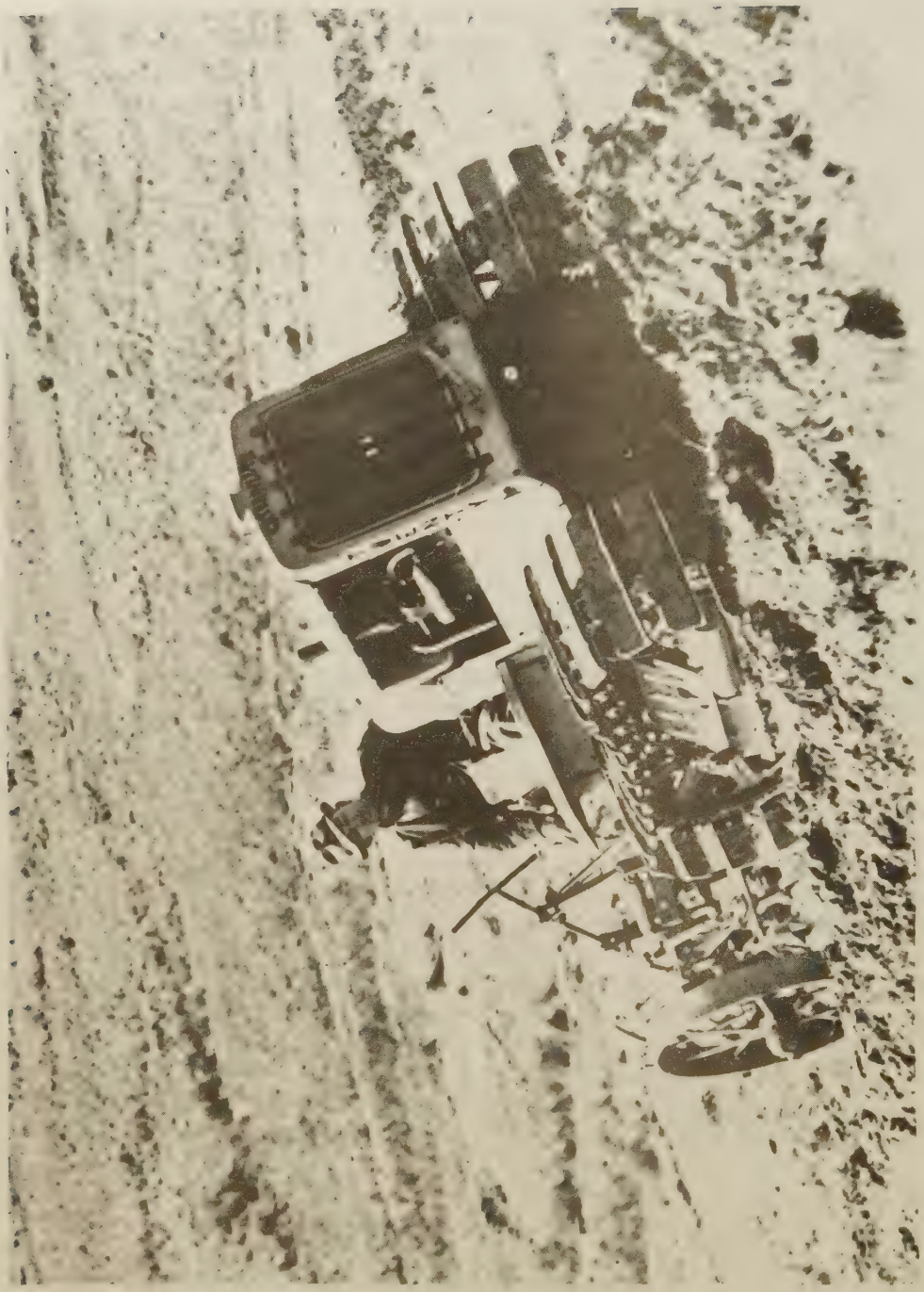
A comprehensive series of seeds mixture trials, reported in Bulletin H No.14 (1936), were laid down for study in upland areas by M.T.Thomas to provide information on seeds mixtures, methods of cultivation an manurial requirements. These experiments emphasized the need for large dressings of Ca and P for satisfactory establishment under these conditions.

One by-product of the work on reseeding was the finding that buried seeds were an important source of weeds which could remain viable for many years in the soil (13).

The campaign for facilities to carry out hill land research was rewarded by the generosity of Sir Julian Cahn, and the Station came into possession of suitable land in 1933 when the Cahn Hill Improvement Scheme began. The land made available consisted of 1,190 ha on the Hafod Estate at Devil's Bridge, extending from about 270-600 m above sea level. This included the home farm, Pwllpeiran, which currently forms part of the Ministry of Agriculture Experimental Husbandry Farm. Some 50 ha of land were also rented in Radnorshire. The aim of the Cahn Hill Improvement Scheme was to demonstrate that large scale hill improvement was practicable "and if agricultural prosperity again becomes a reality the event will prove whether it can be turned to profit".

In 1934, David Lloyd George provided the Cahn Hill Improvement Scheme with financial aid to survey the agricultural and waste lands of Wales and this was published as a map and accompanying book in 1936. The survey showed that a large percentage of the land was under poor grass, but capable of improvement which, according to Stapledon, would enable Wales to double her sheep and cattle population (14).

Some of the most impressive early work was the ploughing up of the lower hill



grazings prior to reseeding. A variety of implements were tried before the most suitable were found for seed bed preparation. It was on such land that Moses Griffith (then Lands Director, Cahn Hill Improvement Scheme) and Stapledon were able to try out pioneer crops on a farm scale, Italian ryegrass and rape being the most popular.

Winter foggage studies were conducted on Italian ryegrass and on grass grown in drills (especially timothy) in the manner developed for seed production. The work emphasized the value of green herbage as compared with "winter burn", and of leaf as compared with stem, and from this the concept of complementary grazing was developed (8).

One of the great features of the C.H.I.S. was that it was possible to report the results in terms of livestock, i.e. number of grazing days, number of lambs, liveweight gain, cost of operations, etc. In this way the results were of direct value to the farmer and their influence on farming practice was very considerable.

In order to study the effect of improvement on the whole farming system, a large experiment was started in 1937 in which small flocks of ewes were grazing for the entire season on the same large plots. The plots were on unimproved swards of different botanical composition and on a reseeded sward. This trial showed the superiority of the reseeded sward in terms of animal production.

The preliminary trial was followed by another which was conducted by Ll.I.Jones between 1949 and 1958. In this trial the native sward was compared with swards reseeded with either commercial or S varieties. The sward sown with the S varieties retained the sown species for a much longer period and was superior in animal production. Complete records of the financial aspects of sheep production were kept, allowing assessment of the value of reseeding in direct monetary returns and its long term effect upon the farm economy. Further details of these investigations, together with those obtained from other studies undertaken on hill land during these early years, have been brought together by Ll.I.Jones in Tech.Bull.No.2 entitled Studies on Hill Land in Wales (1967).

THE WAR YEARS AND POST-WAR PERIOD, 1940-1960

By the outbreak of war, the Station was in many ways prepared as regards what had to be done to increase food production, and the experience gathered by the Department over the previous 20 years was put to use in the field. It could hardly have been foreseen, however, that the team which had been so carefully assembled by Stapledon during the pre-war period would be broken up to form in 1940 the Grassland Improvement Station at Dodwell near Stratford on Avon. Other members of the Department were seconded to County War Agricultural Executive Committees during this period, as a result of which research work at the Station virtually came to a standstill.

The appraisal of varieties based on County (Extension) Trials, together with wartime experience with S varieties, had led to an extensive knowledge of the behaviour

of these varieties, including their reactions under widely differing soil and farming systems. After the war, changes in agriculture created circumstances necessitating a change in agronomy policy, the most immediate need being a re-evaluation of the Station's varieties in relation to the more intensive agriculture of the post-war period. The first five years of this period then saw the sowing of the last of the complex seeds mixture trials at out-centres, and attention was focused on a more critical appraisal of the yield and nutritive characteristics of a smaller number of varieties. The outstanding need was to have strictly controlled management treatments, avoiding differential grazing of varieties and carry-over of fertility. Comparisons were made between the existing S varieties and comparable varieties available on the market; new potential varieties were also studied after the breeder had completed his work on them.

The overall complexity of agronomic evaluation demanded a rational approach, and in 1948 a 3-stage system of variety testing was introduced. Stage I trial was a survey of potentiality which served as a screen prior to more critical evaluation. Large numbers of small plots provided the preliminary evidence on establishment, growth rhythm, aggressiveness, disease resistance, winter hardiness and persistency.

The better varieties were studied further in stage II trials where the influence of management and manuring on herbage production was the most important feature. As many quantitative measurements as possible were taken, using varieties of known performance for comparison and, in general, a range of management and manuring regimes, including grazing by sheep. Observations in these trials were normally recorded over a number of seasons in order to compare annual and seasonal production as well as botanical and chemical composition.

Stage III, based on animal production potential, was reserved for a still more restricted number of varieties. Comparison of S.24 ryegrass and S.170 tall fescue undertaken by Ll.I.Jones with grazing cattle (18) is an example, with performance being recorded in terms of grazing season, liveweight gains and condition of the animals. Restrictions of land resources precluded any extension of this type of direct measurement of animal production, and the number of such trials was very limited.

It was not surprising, under these conditions, that various problems of assessment techniques came under intensive consideration during this period. While sampling procedure, the effect of defoliation height and the significance of differential loss of apices (when cutting varieties of different heading dates) featured prominently, the most crucial consideration concerned the place of the grazing animal in the assessment procedures. The question continually arose whether yield data obtained in the absence of the grazing animal could be regarded as giving a reliable indication of the yields to be obtained under grazing. Using wethers harnessed for the collection of dung and urine, D.G.Miles was able to study the effects of treading and of the nutrient return through the animal in a range of species. The yield of herbage from grazed swards receiving animal returns plus about 90 kg of fertilizer N/ha was equivalent to the yield from cut swards receiving about 225 kg N. In addition to their direct bearing on problems of assessment, trials of this nature contribute also to an understanding of the

behaviour of the grass crop and its responses to various management practices.

This interplay between variety trials, studies of assessment technique and management studies is illustrated by comparison of S.24 and Irish perennial ryegrass by Roy Hughes, published as the last of the series of H Bulletins (No.18 in 1955). Apart from elucidating the appreciable differences between these varieties in the seasonal distribution of yield, and the implications of the greater persistency of S.24, this work showed the sensitivity of Italian ryegrass, sown as a companion grass, to the level of nitrogen manuring.

This is illustrated by the following figures where the persistency of Italian ryegrass is measured by its percentage contribution to the total herbage production.

	Sown with S.24 ryegrass		Sown with Irish ryegrass	
Harvest year	-N	+N	-N	+N
1st (1948)	35	40	51	54
2nd (1949)	8	17	34	58
3rd (1950)	3	6	11	22
5th (1952)	1	2	7	11

The effect of the variety/management combinations on a following oat crop was also studied. Similarly, Ieuan Davies' (17) studies of a range of species and varieties under continuous cutting, although primarily a variety trial, pointed to the importance of harvesting conservation crops at critical stages of stem development, especially with reference to the regrowth characteristic.

In the early 1950s several lines of investigation, which later developed as agronomic guides to plant breeding, continued at extension centres: A. Troughton has studied root development at locations of differing soil type; A.H. Charles studied the population structure of leys at various dates after sowing paired varieties at lowland and upland centres; Miss A.G. Davies collaborated in the work in a survey of the reactions of five perennial ryegrasses under various spacings and with different cutting systems. One development of Troughton's work is the examination of the root/shoot ratio in relation to the productivity of various genotypes, whilst Miss Davies' work led to studies of the interactions of high and low-yielding genotypes under sward conditions.

CURRENT RESEARCH WORK

The last ten years have seen a further intensification of grassland farming - to an extent unthought of in the immediate post-war years, and as a consequence the Agronomy Department has had to reconsider yet again its role and methods of approach. In reorganizing the work, advantage was taken of the opportunity to integrate the programme more closely with the genetic, physiological and breeding research conducted in other Departments at the Station. To achieve a greater agronomic impact on breed-

ing, as well as on evaluation, assessment now proceeds concurrently with, and commences early in the breeding programme. To this end, work has extended to include studies in glasshouses, growth rooms, and, more recently, into animal intake studies. A new appreciation of plant performance and its interaction with the climatic, soil and animal factors prevailing in intensive systems is an essential prerequisite to any further advance through plant breeding.

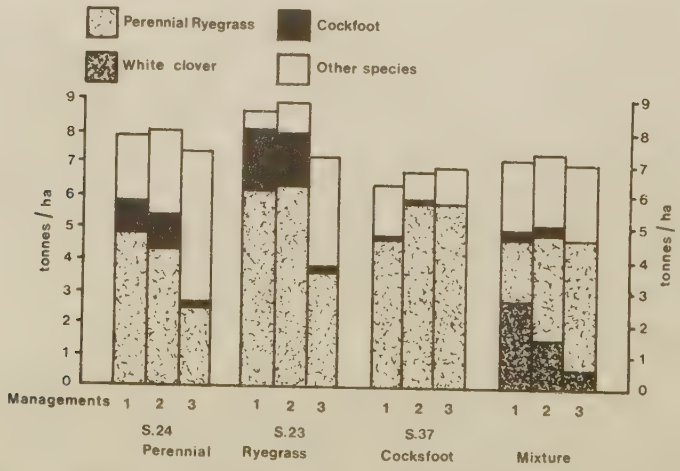
Five main projects are involved:

1. Agronomy of herbage varieties
2. Herbage quality
3. Crop-weather relationships
4. Agronomic implications of variation within varieties
5. Hill-land research

1. The agronomy of herbage varieties

Several major evaluation programmes have taken place in the period commencing with the comparison of the behaviour and production of five grass varieties (Italian ryegrass S.22, perennial ryegrass S.23 and S.24, cocksfoot S.26, and timothy S.48) sown with S.100 white clover (11, 19). The comparisons were made in six different ways, involving grazing or mowing, both with and without dung and urine return or compensatory quantities of artificial fertilizers. The reactions of each species to differences in the management system were marked, ryegrass, particularly Italian, benefiting from grazing and the return of faeces, while cocksfoot responded equally well to cutting and showed little preference for the form of nutrient return. Some of the results are illustrated in Fig.1.

Fig.1. Yield of herbage (t/ha) - average of third and fourth harvest years



Management: 1) grazing with return of dung and urine, 2) mowing with return of equivalent amounts of dung and urine, 3) mowing with return of artificial fertilizers containing equivalent amounts of P_2O_5, K_2O and nitrogen.

This experiment emphasized the close relationship between method of agronomic assessment and type of utilization intended for the variety in farm practice. Over-reliance had been placed, and in some places continues to be placed, on the results of small plot trials carried out largely without the sward-conditioning influence of the animal and harvested by mowing machinery or shears. The importance of this factor cannot be overstressed for it has now become evident that certain varieties, notably late perennial ryegrasses like S.23 which were previously regarded as lower yielding, are in fact superior under intensive grazing management to varieties with fewer inherent survival mechanisms.

In 1960 results were published of the assessment of twenty-four varieties of perennial ryegrass from Europe and the British Isles (20). In the early group, S.24 and Devon Eaver surpassed all other varieties in spring production, while the continental varieties were capable of higher summer production. In the late-flowering group, Ba 6293 (S.321) showed outstanding seeding year and subsequent spring and autumn production, while S.23 again showed highest persistency under rotational sheep grazing and one silage cut.

At this time, increasing attention was being paid to the possibility of out-of-season production, particularly at the Grassland Research Institute, Hurley, and the Plant Breeding Institute, Cambridge, and in 1961 and 1962 members of the Agronomy Department joined plant collection expeditions to the Iberian Peninsula, Algeria and Morocco. Material collected during these and subsequent expeditions formed the basis of breeding programmes, but trials to evaluate two synthetic tall fescue varieties developed at Cambridge from plant material collected at high and low altitudes in Morocco, and cocksfoot varieties bred at the Station from S. European material, indicated a number of limitations to the progress possible from direct use of introductions from these centres. In particular, a marked lack of winter hardiness was recorded, and the two severe winters of 1962-3 and 1968-9 pinpointed a number of factors affecting winter survival of swards. In many respects the damage to grasses was more severe in the most recent instance, probably as a result of the increased nitrogen usage on farms and difficulty of controlling an autumn flush of growth. The grasses most adversely affected during the 1962-3 winter were Italian and short-rotation ryegrasses, particularly those of maritime rather than continental origin. Timothy was the least damaged of all the grasses, S.51 in particular showing very early spring growth after a severe winter.

S.170 tall fescue also has high potential for early spring production, particularly in upland areas. It is exceptional in being perennial and leafy without the normal coarseness associated with the species. Trials completed in 1960 (21) showed that once fully established, its relative production in early spring was often better than that of Italian ryegrass and always better than of S.24 ryegrass. Tall fescue is poor in establishment vigour, especially when sown with other species or where low seed rates are used.

Field studies of the intergeneric hybrid developed from the cross between S.22 Italian ryegrass and S.170 tall fescue were initiated in 1964 (30). Five objectives were set

out in the scheme designed for agronomic evaluation of the new grass, namely:-

(a) to examine the agronomic characters of the new material;
(b) to indicate at an early stage where further selection was required;
(c) to provide for the breeders data and plant material obtained by channelling the variation through sward pressures and from micro swards;
(d) to provide data indicative of the type of management most appropriate for maximizing the potential of the varieties;
(e) to develop rapid screening techniques applicable to the type of material.

These aims indicate the general approach in providing guidance to the breeder.

In the experiments, the new hybrid was studied in comparison with the parent varieties and in its unselected form was found to be only marginally better than the tall fescue in establishment vigour. An examination of single plant material, however, has revealed a proportion of more prostrate, narrow leaved, higher-tillering types, and also of high tillering types within the large-leaved group (31).

The whole problem of grassland establishment formed the basis of a series of agronomic studies undertaken by A.H. Charles. Field trials on a country wide basis showed that in practice a rapidly developing ley could produce as much starch and protein as an average crop of oats plus the undersown herbage (3). The use of a cover crop for grazing or silage resulted in reduced yields in July and August, the period when production from maiden seeds is vital. With increasing nitrogen use on cereals, clover in particular is severely depressed.

Increased nitrogenous manuring of pure grass swards under farm conditions has highlighted further problems for detailed agronomic investigations. Comparisons were made in 1960 and 1961 of the yields and chemical composition of S.23 and S.24 perennial ryegrass, S.143 cocksfoot and S.48 timothy under a seven-cut-system (24). Nitrogen in the form of nitrate of soda, sulphate of ammonia or urea was applied at the rate of 90 kg N/ha per cut. Yields were increased by as much as 400%, giving an average response of 14 kg herbage dry matter per 1 kg N applied. Subsequent experiments have given yields closely parallel to those achieved under simulated sward conditions (Developmental Genetics report). Although they appear very high in comparison with records made in the period before intensification, there is now ample evidence that annual yields of over 17,000 kg DM per ha are being utilized under paddock grazing systems on farms.

The question of sward survival is extremely important in these high productivity systems. It has become apparent that ryegrasses with the persistency of S.23 are necessary to sustain production from year to year without reverting to ploughing and reseeding. Even in the case of S.23 the extremely severe winter of 1968/69 led to extensive mortality of swards where 400 kg N/ha were being used annually.

Few modifications have been made since 1959 in the field techniques of variety evaluation, although mechanization has been increasingly introduced in place of the use of hand shears for yield sampling. Many changes have taken place, however, in

the approach to designing management treatments. Attempts at further sophistication through the application of an electronic pasture sampler, developed at U.C.N.W., Bangor, on the capacitance probe principle, proved disappointing (27). Poor results were obtained when the dry weight comparison was between different varieties of one species, and where the general difference was small. Where assessment was being made on morphologically similar varieties, or a range of treatments on only a few varieties of close similarity, the meter offered a more objective and accurate assessment than visual scoring.

An important aspect of the agronomy of herbage varieties is concerned with the difficulties of interpreting sward behaviour in terms of quantity and quality, the quantitative description of variety models and the realization of more objectivity in management on the farm. Notable contributions have come from the work of Ieuan Davies published in 1969 as Technical Bulletin No.3 entitled The Influence of Management on Tiller Development and Herbage Growth. These studies developed from investigations started in the early 1950s on varieties and their management in grass drying systems. Attention was focussed on the relationships in time between reproductive differentiation, the beginnings of internode extension and elevation of the stem apex above defoliation height, and head emergence. Studies of swards derived from different grass varieties have shown that there exists a distinct group of tillers differing by no more than 3 weeks in the time of attaining any specific stage of development. Successful management of the crop in spring hinges on an appreciation of this characteristic, for example, defoliation immediately prior to elevation of the apex of the most forward stem tiller results in a harvest of leafy material whereas defoliation 3 weeks later gives a crop of immature stem tillers. Defoliation immediately before and during this 3-week period should be avoided since the youngest leaves of the tillers with apices below defoliation level are removed, which results in the rapid development of stems in the regrowth. For a conservation crop the 3-week period referred to should fall roughly in the middle of the rest interval if yield and quality of the crop is to be maximized and a rapid regrowth ensured.

Detailed analyses of stems at flowering have revealed that the youngest (uppermost) internodes are lower in digestibility than the oldest basal portions. Silicification is more extensive and lignification more rapid in the upper internodes. This may be significant in terms of high yield responses to N applied shortly before stems begin to develop. The timing of N applications has also been examined with respect to accelerating the initial stages of stem development and stimulating secondary tillering. In this connection differences in growth rhythm and heading date may give widely different responses between grass varieties when N is applied at a specific date in spring. Since the yield and nature of a mid-May cut, the immediate regrowth, and the subsequent midsummer production are all affected, an appreciation of these factors is clearly essential to a correct interpretation of variety trials.

The life-span of the leaf blade determines when the blade makes a positive contribution to the yield of herbage and the period during which characteristics important in feeding value are retained. Appreciable species differences occur; the large leaves

of tall fescue, for example, are longer-lived than the smaller leaves of perennial ryegrass. The application of N reduces leaf longevity in all species and can be attributed primarily to the influence of increased apical activity leading to accelerated senescence. These studies are being continued with emphasis on anatomical aspects of leaf development and will form an essential link between the agronomy of the standing crop and the studies of its feeding value and intake characteristics described below.

2. Herbage quality

Prior to 1959 most of the attention in herbage plant breeding was devoted to increasing total and seasonal productivity and rather less to the ultimate value of the herbage in terms of meat, wool and milk production. Although leafiness was always high in breeding priorities, its full significance was not established until the development of the in vitro digestibility technique at Hurley (15) provided the necessary method for measuring nutritive value on an extensive scale. Studies in the Developmental Genetics and Chemistry Departments (23) revealed the extent of genetic variation in nutritive components such as digestibility, water soluble carbohydrates and crude protein, within and between ryegrass and cocksfoot varieties, and the possibility of response to selection for these attributes.

A major contribution of the Agronomy Department (in collaboration with Chemistry) has been the study of the seasonal pattern of variation in these three factors over a wide range of species and varieties. During 1961 the Department was equipped with a small animal unit and refrigerated herbage store which made possible the inception of a programme of digestibility determination in vivo. Rumen fistulated sheep of the same breed provided the necessary liquor for parallel in vitro tests. The first results substantiated the evidence from the Grassland Research Institute that (a) digestibility remains fairly constant until ear emergence after which it falls rapidly, and (b) the digestibility of ryegrass is always higher than that of cocksfoot at similar stages of maturity (22).

Varietal and seasonal trends in digestibility, crude protein and water soluble carbohydrate contents have been studied in a wide range of grasses and detailed investigations have been undertaken into the effect of management and fertilizer practice on these attributes.

Detailed morphological examination of the same plant material indicated that the prediction of digestibility in the field, based on leaf content, is more accurate than prediction from the calendar date or stage of growth. By this means, crops of S.24 ryegrass, S.37 cocksfoot and S.51 timothy were harvested at nearly identical dry matter digestibilities of 70 per cent, for use in feeding trials. A grass drier made possible the conservation of large quantities of these and other feeds, without further deterioration in quality, for larger scale experimentation with the Station's existing sheep and cattle stock.

Results obtained in preliminary feeding trials conducted in 1964-66 justified cert-

ain conclusions regarding the relationship between some aspects of herbage quality and animal performance. Although the liveweight gain of animals depended largely on their intake of digestible dry matter, it was apparent that this intake was not invariably governed by the digestibility of the feed. Furthermore it appeared that some grass varieties, even though well fertilized when put up for conservation in early spring, may produce crops which do not contain adequate protein or minerals to support the animal production which is theoretically possible from crops of high digestibilities.

The results of one study involving 9-12 months old cattle are shown below; average feed intake (DMI) and liveweight gain (LWG) are given in kg per day.

	Without red clover		With red clover	
Feed	DMI	LWG	DMI	LWG
S.24	4.89	0.31	6.52	0.73
S.22	4.89	0.34	5.84	0.68
S.37	5.16	0.62	6.47	0.72
S.51	3.85	-0.03	6.07	1.04

The intake of S.51 timothy was significantly lower than that of the other three grasses and animals failed to achieve any gain in weight. Larger steers eating S.37 cocksfoot, on the other hand, made appreciably better gains than on either S.24 or S.22 ryegrass, exceeding 0.9 kg/day with a conversion factor of 7.7 kg grass dry matter per 1 kg liveweight gain. Both clover and regrowth supplements led to compensatory gains in the animals originally offered the poorer feeds. The crude protein level in S.51 timothy was only 6%, well below the recommended standards(1).

In 1966 further crops were harvested and in this case two S.51 feeds of 10.6% and 13.8% crude protein respectively, were offered to steers and wether hoggs. Improved gains were obtained with the second feed.

Studies of dry matter/digestibility relationships are very relevant in estimating animal production potential per ha. Established swards of ryegrass, cocksfoot, timothy and tall fescue receiving over 300 units nitrogen all yielded upwards of 14,500 kg dry matter at digestibility levels of 70% or over. Late flowering varieties within a species were superior at the highest digestibility levels.

A large scale survey of the intake characteristics of a large number of herbages is in progress in collaboration with the Chemistry Department. Examinations are made of the physical and chemical features of feeds which show departures from expectation.

3. Crop weather relationships

Progress in micro-climate investigations with herbage swards has been limited by difficulties of instrumentation, but some progress has been made in studying light and temperature distribution in canopies of contrasting grass species, particularly in rela-

tion to different rates of establishment from seed, e.g. S.22 Italian ryegrass and S.170 tall fescue. Amounts of short-wave radiation reflected by different canopies depend largely on the angle of incidence, and can range in autumn from 18% to over 40%, according to the time of day.

The immediate hinterland of Aberystwyth provides a ready means for the study of herbage over a wide altitudinal range. Crop weather stations have been maintained over a number of years up to altitudes of approx.520 m where the rainfall exceeds 2,500 mm per annum. In a study of herbage production from eight grasses at Tynpynfarch (210 m) and Gogerddan (30 m), under heavily fertilized conditions, the average yield was 45% greater in the lowland. S.59 red fescue, however, only produced 18% more herbage in the lowland (7).

Soil transfer experiments (25, 29) have underlined the importance of climatic as distinct from soil factors in the reduction of yield with altitude in the western areas of Britain. Differences in spring growth are shown in Fig.2. Continuous recording of incoming solar radiation, temperature, rainfall and wind run has provided the necessary information for the calculation of Penman's potential evaporation and transpiration at four meteorological stations on an altitudinal transect 40 km long, traversing the Pumlumon range from west to east.

Incoming radiation and net energy were found to decrease markedly with altitude to the west but remained high in the rain shadow to the east. Conversely, the wind component increased on the sites with a western exposure resulting in a very high theoretical transpiration rate which was not reflected in plant growth rates when a bioassay with a single S.24 ryegrass genotype was carried out (32).

A further aspect of investigation with significance to pasture plant breeding has been the measurement of the crop resistance to drying during haymaking. Increasing fertilizer use has added to the difficulties of conserving a product of high feeding value in western Britain. During June 1967 the crop resistance was measured in two contrasting varieties, S.37 cocksfoot and S.215 meadow fescue (33), and differences in rate of drying were recorded. Subsequently, the effect of tedding and crushing swaths of S.23 ryegrass was examined in relation to the rates of moisture loss and the prevailing weather.

4. Agronomic implications of variation within varieties

Genotypic variation within swards and its agronomic significance in relation to yield and survival has received considerable detailed attention throughout the period. It was discovered that extensive changes took place in the composition of swards when they were subjected to contrasting managements, particularly during establishment (2). During the two months following the sowing of a seed mixture the surviving grass seedlings represented only 20% of the viable seed sown. By the end of one year there was a further reduction to approximately 10%.

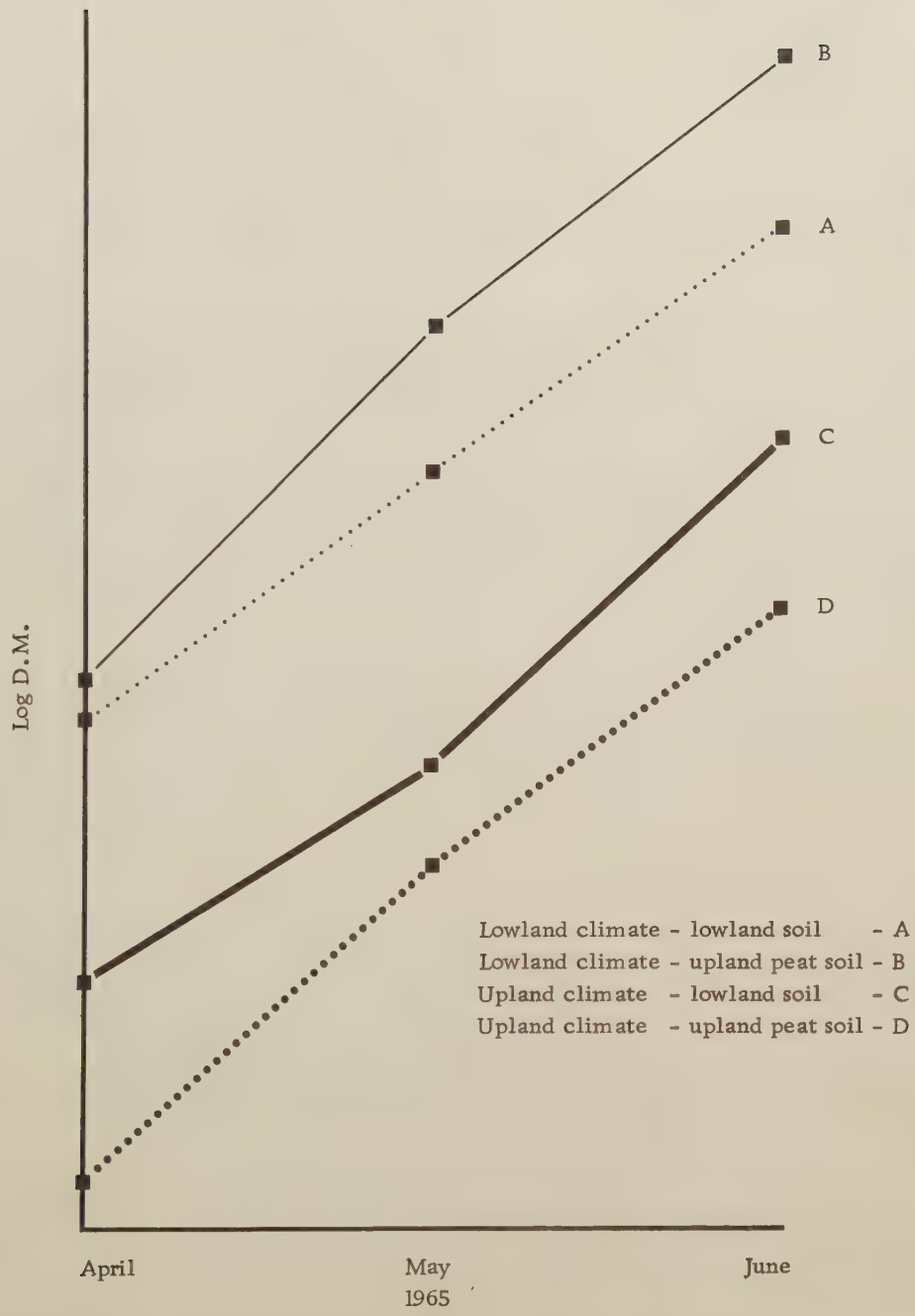


Fig.2. Dry weight/plant. Mean of S.23, S.170, S.59

The response of mixtures of perennial ryegrass, cocksfoot and timothy varieties to various selection pressures was traced over a period of three years by examining survival material under spaced plant conditions. Hay management encouraged the domination of varieties bred for hay purposes and grazing management the domination of pasture varieties. Edaphic factors, especially soil nitrogen and moisture status had further appreciable effects on the balance of sward composition. Studies of natural ryegrass populations from the Monmouthshire Moors, carried out in collaboration with the Herbage Breeding Department, revealed a high correlation between the yield of individual genotypes as spaced plants and the fertility of the collection areas. These findings have obvious significance in breeding policy and underline the value which controlled natural selection can have in speeding up breeding programmes in the future.

Under hill land conditions, and even in the lowlands during abnormal years, winter mortality also accounts for rapid change in the varietal and genotypic composition of swards. Surviving plants, collected after the swards had been exposed to the successive hard winters of 1961 and 1962 at Syfydrin (330 m), were examined and compared with the original varieties during the relatively open winter of 1964. High mortality had occurred in the early genotypes, particularly in S.22 and New Zealand perennial ryegrass, but also to a notable extent in persistent varieties such as S.23. As a result, spring production was lower in the survival material. In S.345 cocksfoot, however, winter damage is normally high in hill areas, and the survivors were on average more productive in spring (28).

The screening effect of the hill environment was used as a method of channelling variation in a Portuguese cocksfoot introduction (Bc 4651) and a continental selection of Phalaris arundinacea (Bs 2778). Cocksfoot genotypes which had survived through the winter at Syfydrin showed only 10% mortality in a growth room at -6°C compared with 80% in the original stock (26). The use of controlled selection pressures also has proved effective in improving establishment vigour in the S.22 x S.170 hybrid, and tolerance of heavy nitrogen dressings in white clover (31).

In more fundamental studies in the glasshouse, growth room and in the field, wide variation was noted in the reaction of grass genotypes to different levels of mineral nutrition, defoliation treatment, soil moisture level and the carbon dioxide concentration of the atmosphere. Measurement techniques have been developed to study various components of growth, including individual plant yield, root/shoot ratio, tiller number and size, and ratio of barren to fertile tillers. Computer programmes have facilitated the analysis of the data collected from the large numbers of plants involved (16).

The variation in shoot growth between genotypes of Irish and S.23 ryegrasses grown in nutrient solution was due to differences in the rate of production and size of tillers. Differences in root growth and root/shoot growth relationship were due to the size of individual roots. In both varieties root characters were found to be more variable than shoot characters, demonstrating the strong selection imposed on the latter by breeding and management. When nutrients are non-limiting and carbohydrate reserves

adequate, plants with a low root/shoot ratio would not be at a disadvantage. Under stress, the possession of a large root system appears desirable. It was found that increased mineral nutrition increased the genotypes' shoot growth and reduced the root growth, resulting in greater susceptibility to winter damage, drought and defoliation losses. The increased shoot growth resulted from new tiller production and increased tiller size under spaced plant conditions, whereas under competition only tiller number increased and tiller size decreased or remained constant. Plants with contrasting growth characteristics have been selected for further studies.

Complementary studies of other components of growth and their influence on yield pattern have provided more precise information on the behaviour of varieties at different times of the year. Dry weight increase in early and late varieties of ryegrass and cocksfoot takes place from the last week in March in normal years (5). The early flowering varieties do not produce more above ground herbage at an earlier date than the late flowering varieties. The earlier onset of leaf and stem elongation, however, results in greater yields above a utilizable height.

Tillering increases with rising temperatures and greater nitrogen availability, particularly in pasture varieties like S.23. High tillering capacity in late varieties leads to higher utilizable yields where winter damage has been severe in early types. In pasture systems, regrowth is more important than differences in primary growth and more attention is being paid to this subject. Swards of four ryegrass varieties were subjected to different dates and frequency of cutting. For a given variety there was a good correlation between regrowth and both tiller number and weight of leaf blade remaining after cutting (4).

Selection of genotypes for rapid regrowth characteristics has resulted in higher levels of water soluble carbohydrates in the stubble.

5. Hill land research

The improvement of hill land continues to receive considerable attention from the Grassland Agronomy Department.

Research since 1959 has concentrated on three major aspects:

(i) the measurement and evaluation of the factors of climate, soil and native vegetation which limit production;

(ii) the potential for breeding grass and legume varieties for these conditions, and

(iii) the integration of improved areas into the overall hill farm ecosystems.

Progress in obtaining information with wide applicability in the hill areas of Britain was aided by the acquisition of several small experimental areas in 1960, and a 34-ha Hill Centre at Pant-y-dŵr in Radnorshire in 1964. This provided both climatic and soil sequences typical of areas with varying potential for improvement, supporting native vegetation ranging from Agrostis-Festuca through Nardus and Molinia to Trichophorum, Erica, Polytrichum and Eriophorum.

Continuous recording of climatic factors at all sites has allowed interpretation of plant responses to temperature and solar radiation patterns in the uplands. In general, it can be concluded that high rainfall and low radiation severely limit potential production above that altitude where rainfall exceeds 1500 mm per annum. A major contributing factor is winter frost damage and consequently winter-hardiness is the prime requisite in new varieties.

Preliminary screening of an extensive range of species and varieties since 1961 revealed that only red fescue, timothy, white clover and, to a lesser extent, tall fescue had any potential on wetter organic soils. Closer examination of red fescue has shown that it compared favourably with perennial ryegrass in yield, particularly under stress conditions in spring and where fertilizer application is limited (35). Overall digestibility is slightly lower, however, and efforts are being made to improve this feature in S.59 red fescue by selection for later heading genotypes.

Comparative yields from Syfydrin are shown below (S.59 high lime = 100)

	Low lime	Intermed. lime	High lime	Mean
S.59 red fescue	72	99	100	90
S.50 timothy	56	62	77	65
S.23 ryegrass	53	74	73	65
S.59 + S.48 (timothy)	69	92	100	87
Mean	62	82	87	

Comparative soil studies have emphasized the extreme deficiency of available nitrogen in many hill soils (34). This factor, above all others, limits production but there is limited scope for increase in fertilizer usage except on freely drained soils. On peat land only approximately 30% of applied nitrogen is recovered by the grass sward and the establishment of functional white clover is essential. With adequate lime, phosphate and potash S.184 wild white clover has contributed over 270 kg N/ha when expressed in terms of dry matter. Its value as a protein, mineral and energy source to livestock is even greater, and its introduction by surface seeding on the upper parts of the hill farm is being studied with a view to providing information on the integration of improved land with unimproved hill.

FUTURE DEVELOPMENTS

The plant breeders' challenge is to improve the herbage - the main raw material in various livestock systems. Since the soil, the sward, the atmosphere and the animal are closely involved, a multi-discipline approach has to be applied to various parts of the production chain. One of the functions of the agronomist is to describe herbage variety models specifically designed for different systems of utilization. When various animal production targets are set, the question is what kind of herbage is required to ensure their economic achievement?

The other main function of the agronomist is to evaluate all promising new material developed by the breeders. It is not so very long ago that a variety could be reasonably evaluated by describing its botanical characteristics, including a few ecological reactions. As previously indicated, the presence of the grazing animal in grassland experimentation and evaluation of new breeders' material is considered an essential feature of assessment. In evaluation schemes, despite the inherent problems, the assessment of varieties for the grazing systems of today demands the presence of grazing animals somewhere in the scheme; the problems have never been more acute, since the small scale simulation of highly intensive systems has not proved possible as yet.

The current and future situations, therefore, demand a comprehensive field assessment based on a concept of the effect of management stresses imposed by the system on the sward, on the animal and on the farmer, in terms of complexity and difficult decision making in relation to stock and grassland management. Assessment of the biological potential of material, therefore, is only part of the problem. If the plant breeder is to contribute to the simplification of live-stock systems, this will not be achieved by considering yield for its own sake, even when attributes of high feeding value are built in. Some systems, where soil conditions, animal treading and inclement weather are significant features, demand flexible varieties that can act more effectively as buffers to these various stresses; this being a biological approach to reducing the weather dependence under which most live-stock enterprizes operate, and increasing management objectivity. Thus, herbage varieties cannot be considered in isolation from their management, especially where grazing is involved.

Much of the work of the Department will continue to be devoted to describing problems and regimes as they exist in the field, in terms meaningful to the breeder and physiologist and relevant to the agricultural ecosystems to which our research studies apply. Means will be sought to improve the evaluation of the material at all stages - from early in the breeding programme to the 'final' assessment of the potential variety.

Preparation has to be made for the testing of varieties which will be developed on the basis of improved physiological efficiency. Irrespective of the outcome of the routine agriculturally-orientated evaluation, the breeder/physiologist will wish to know whether the physiological model has been achieved, when judged on a field scale. This will involve the relationship between the crop, its immediate environment and the weather. Studies of microclimate factors will be pursued on the basis of surveys of the relationships between these and the morphology and geometry of contrasting varieties, and on contrasting swards of the same variety.

Comparisons of local mesoclimates will continue in the context of site evaluation, and will be related to studies of rates of field drying of herbages for conservation, where the aerodynamic situation prevailing seems to override all others. When one considers the importance of conservation in the humid west, it is of some concern that previously so little attention has been expressly paid to it under the very conditions that create the problems.

The morphological and physiological basis of growth and regrowth has been studied in relation to the effects of nitrogen, season and management, in order to determine how yield is built up in variety/management combinations. Work on the life history of various plant organs under a range of field conditions has revealed the details that need to be examined further. It is interesting to speculate that from such studies the basis of management objectivity could well be derived. We can already predict in the field the energy value of a standing crop for conservation, and the size and quality of the regrowth, provided certain constraints are known. The projection of such work involving a combination of studies of the agronomy of varieties, and single grass variety swards for animal intake studies will be given a high priority, the ultimate aim being to make simplified predictive devices workable on a farm basis.

Related to the above studies are considerations of the extent and implication of the inherent variation of certain morphological characteristics and physiological responses found within varieties. Their plasticity, both singly and in combination, is an important avenue of study for both breeders and agronomists, especially with regard to varieties for future grazing systems. While flexibility over the whole range of agricultural usage is not envisaged, the versatility of S.23 ryegrass as shown by its superior performance, extending from the wet hill farms of Wales to the intensive dairy farms in S.E.England, is of considerable interest.

Over the years, routine variety evaluation trials have contributed greatly to agronomic knowledge in the Station, and they are now regarded as being multipurpose. Every opportunity will be taken to use these trials, where feasible, to examine simultaneously the sward problems relevant to intensive grazing systems and the techniques of screening *per se*. When the subjection of three varieties of Italian ryegrass to three heights and three frequencies of cutting can produce a range of annual output from 10-21,000 kg/ha dry matter, it completely underwrites our emphasis on management treatments in variety evaluation schemes. When one of the three varieties is better than the others in virtually all the nine treatment combinations, the search for the basis of such flexibility is stimulated.

Accepted agronomic tenets seem to be breaking down frequently on intensive paddock systems, which is not surprising when one considers the vast difference in the soil-sward-animal complex of experiments of 20-30 years ago compared with grassland farming of today. We need to know more about the interface between the soil and the tiller - in terms of persistency, abnormalities of growth and utilization factors. The physics and biology of soils have taken on a particular importance in relation to the efficacy of varieties, and consideration must be given to soil compaction, moisture infiltration rates and the decomposition of plant parts and dung.

Paddock systems using beef cattle have already been set up on two different soils to provide the ecosystem for these and related studies. It is important that the paddock should be as similar as possible to those found in a farm situation and accordingly steps are taken to avoid a text book approach to managing the experimental paddocks. In 1969, despite a late turnout (first week of May), 740 kg/ha of liveweight gain was

produced with an input of 220 kg N/ha, and most of the problems of utilization and growth abnormality have been manifest.

Herbage quality is studied jointly with the Chemistry Department and will be concerned with studying the standing crop of single grass variety swards and feeds derived from them at different levels of digestibility. In future other criteria related to crop age will be examined, but the end point will continue to be the elucidation of the chemical and physical factors controlling animal intake. The Agronomy Department will be concerned with the physical factors that can be related back to the morphology and physiology of the crops from which the feeds were derived. Particular attention will be devoted to stem fractions, especially where these limit the voluntary intake below expectation, and we are pursuing techniques of separating leaf from stem in sufficient quantities to allow various admixtures from different crops and species in an effort to elucidate the basis of the problem. Preliminary studies have already begun on S.22 Italian ryegrass and S.51 timothy.

Although some workers have stated that clover has a decreasing importance in the light of high N usage, it could be stated equally strongly that it has an increasing importance. Problems, particularly concerning minerals, that could arise from whole farms sown to just one variety of grass, have been raised. Over the last three years our own work has highlighted problems of realising the energy potential of highly digestible herbage from pure grass swards and the enhancing effect of supplementing such feeds with clover. In intensive systems clover is needed as a nutritional buffer rather than as an N-fixer. Large-leaved and longer-petioled varieties are already on the market and more will follow. Clover will still feature in our grass evaluation trials; the evaluation of the clover *per se* is still fraught with problems, but we have already worked on techniques of studying clovers as single ramets and in large plots, so that their response to competition from vigorous grass can be examined in relation to fertilizer N and urine.

Hill-land studies, conducted mainly at Pant-y-dwr, will continue on the basis of a more precise definition of the climatic, soil and plant factors restricting grassland output in the hills and uplands of Britain. The biological basis for economic improvement of hill farming lies in pasture improvement. This is nowhere better demonstrated than by practising hill farmers in Mid-Wales. As a result of earlier work at the Station and the faith and enthusiasm of the farmers, the success of ploughing and reseeding the better hill land has itself led to a switch of emphasis to wetter sites where all the problems are greatly magnified. These soils are incapable of economic improvement by conventional methods and radical changes in approach to their development have been necessary.

Attention will be focussed on the importance of seasonal water-logging and low biological activity in these soils, and on a point not given particular attention in the past - the low level of available N over a whole range of soils. The prime consideration will be the introduction and maintenance of viable white clover populations (a completely different model to that referred to for the lowlands).

As far as it can be judged at present, economic usage of fertilizer N can only be practised on the better soils. Work started on an academic footing to study the effects of small to massive injections of N into the ecosystem has rapidly assumed more practical importance in view of developments in the hill farming industry. The need for bigger ewes, more and bigger lambs and an increase in output of fat lambs has focused attention on the potential and limits of intensifying production from ffridd and enclosed land on mineral soil. The main problem involves the weather, giving large differences in responses from year to year in spring and summer; e.g. an area of ryegrass giving 11,000 kg/ha dry matter from 280 kg N/ha, gave little more than half that output the following year. The further investigation of these problems is obviously important from ecological and agricultural points of view.

Work on ryegrass, tall fescue, timothy, red fescue and white clover will form the basis of studies designed to improve spring keep and the summer nutrition of hill livestock. The high versatility shown by red fescue over a whole range of conditions has already stimulated work on how establishment and utilization can be improved by breeding. The variety model is such that it would also have a high potential for amenity purposes. Recent comparisons between S.59 red fescue and S.23 ryegrass, including lamb performance, have given a more precise assessment of these problems and the continuation of this work is essential.

It is obvious from the foregoing that a great deal of attention will be paid to improving our understanding of factors concerned with production, utilization and persistency in grazing systems. Persistency itself is of paramount importance and has to be reassessed in the modern idiom, particularly in terms of the variety.

References

(1) Agricultural Research Council, 1965, The nutrient requirements of farm livestock. No.2, Ruminants. A.R.C., London.

(2) A.H.Charles, 1964, J.Br.Grassld Soc. 19, 198-204.

(3) A.H.Charles, 1965, J.Br.Grassld Soc. 20, 241-247.

(4) Alison Davies, 1966, J.agric.Sci., Camb. 67, 139-144.

(5) Alison Davies and D.M.Calder, 1966, Symp. Agric. Met.No.9, Aberystwyth (mim).

(6) W.Davies, 1925, J.Min.Agric. 32, 106-116.

(7) W.I.J.Davies, 1962, Ph.D.Thesis, Univ.Wales (unpublished).

(8) Moses Griffith and P.M.G.Hutton, 1936, Welsh J.Agric. 12, 126-130.

(9) Ll.I.Jones, 1934-36, Welsh J.Agric. 10, 246-265; 11, 96-120; 12, 139-157.

(10) M.G.Jones, 1928, Welsh J.Agric. 4, 183-206.

(11) D.G.Miles, 1960, Proc.8th Int.Grassld Congr., Reading, 112-115.

(12) W.E.J.Milton, 1940, J.Ecol. 28, 326-356.

(13) W.E.J.Milton, 1948, Emp.J.exp.Agric. 16, 163-177.

(14) R.G.Stapledon (ed) et al, 1936, A Survey of the Agricultural Wastelands of Wales. pp.158, Faber and Faber, Ltd., London.

(15) J.M.A.Tilley and R.A.Terry, 1963, J.Br.Grassld Soc. 18, 104-111.
(16) A.Troughton, 1966, Trans.Comm.II and IV Int.Soc.Soil Sci., 385-391.
(17) 1958 Welsh Pl.Breed.Stn Report for 1950-56, 107-111.
(18) 1959 Welsh Pl.Breed.Stn Report for 1956-58, 55-56.
(19) 1960 Welsh Pl.Breed.Stn Report for 1959, 43-45.
(20) 1961 Welsh Pl.Breed.Stn Report for 1960, 53-55.
(21) 1961 ibid., 55-59.
(22) 1962 Welsh Pl.Breed.Stn Report for 1961, 76-77.
(23) 1962 ibid., 145-156.
(24) 1964 Welsh Pl.Breed.Stn Report for 1963, 71.
(25) 1965 Welsh Pl.Breed.Stn Report for 1964, 82-84.
(26) 1966 Welsh Pl.Breed.Stn Report for 1965, 23-26.
(27) 1966 ibid., 67.
(28) 1966 ibid., 72-73.
(29) 1966 ibid., 73-74.
(30) 1967 Welsh Pl.Breed.Stn Report for 1966, 87-91.
(31) 1968 Welsh Pl.Breed.Stn Report for 1967, 51-52.
(32) 1968 ibid., 63-65.
(33) 1968 ibid., 66-67.
(34) 1968 ibid., 69-70.
(35) 1968 ibid., 70.

SEED MULTIPLICATION AND HERBAGE SEED RESEARCH

D.J. GRIFFITHS

H.M. ROBERTS

The Seed Multiplication Department was initially established to assume responsibility for the controlled multiplication of basic seed stocks of the Aberystwyth bred varieties of grasses, clovers and oats and their distribution to the Seed Industry for further propagation. The first varieties of grasses were released to the Seed Trade for multiplication in 1931 and in the course of these early activities it soon became evident that considerable research work into the principles underlying herbage seed production was also required. Accordingly the Department developed its dual role of assuming responsibility for the production of a regular flow of Breeder's and Basic seed stocks of all the Station bred varieties to the seed growing industry, and the conduct of research into topics related to the objective of developing more efficient seed production techniques. Early researches concentrated chiefly upon such aspects as seed crop establishment, seed rates, row spacings, manurial requirements, managements, methods of harvesting and seed storage, but more recently the scope of the Department has been further expanded to include biochemical projects as well as selection studies concerned with the fundamental bases of seed productivity. Some aspects of developments in both these fields of seed multiplication and research are presented below.

REVIEW OF DEVELOPMENTS IN SEED MULTIPLICATION

1. Herbage varieties

Although basic seed stocks of a number of the now well known S varieties became available in the early 1930s, initial interest in their seed production was limited until just a few years before World War II when a small nucleus of seed producers commenced the production of Certified Aberystwyth Seeds. However, the abrupt termination of seed imports in 1940 created the urgent need for home-grown supplies and this resulted in a rapid rise in the areas devoted to the Aberystwyth varieties grown for seed, progressing from about 405 ha in 1940 to over 14,580 in 1947. With the resumption of free seed importations after World War II, increases in subsequent years were less spectacular, but nevertheless, as shown in Figs 1 and 2, they represent an increasing interest in the production and usage of Aberystwyth varieties. When the most commonly used herbage species are considered (perennial and Italian ryegrass, cocksfoot, timothy and meadow fescue), it will be noted from Fig. 2 that the contribution of Aberystwyth varieties to total usage of seed of these species has increased from 8 to 38% over the last twelve years.

Fig.1. Aberystwyth varieties. Inspected 1940-1969.

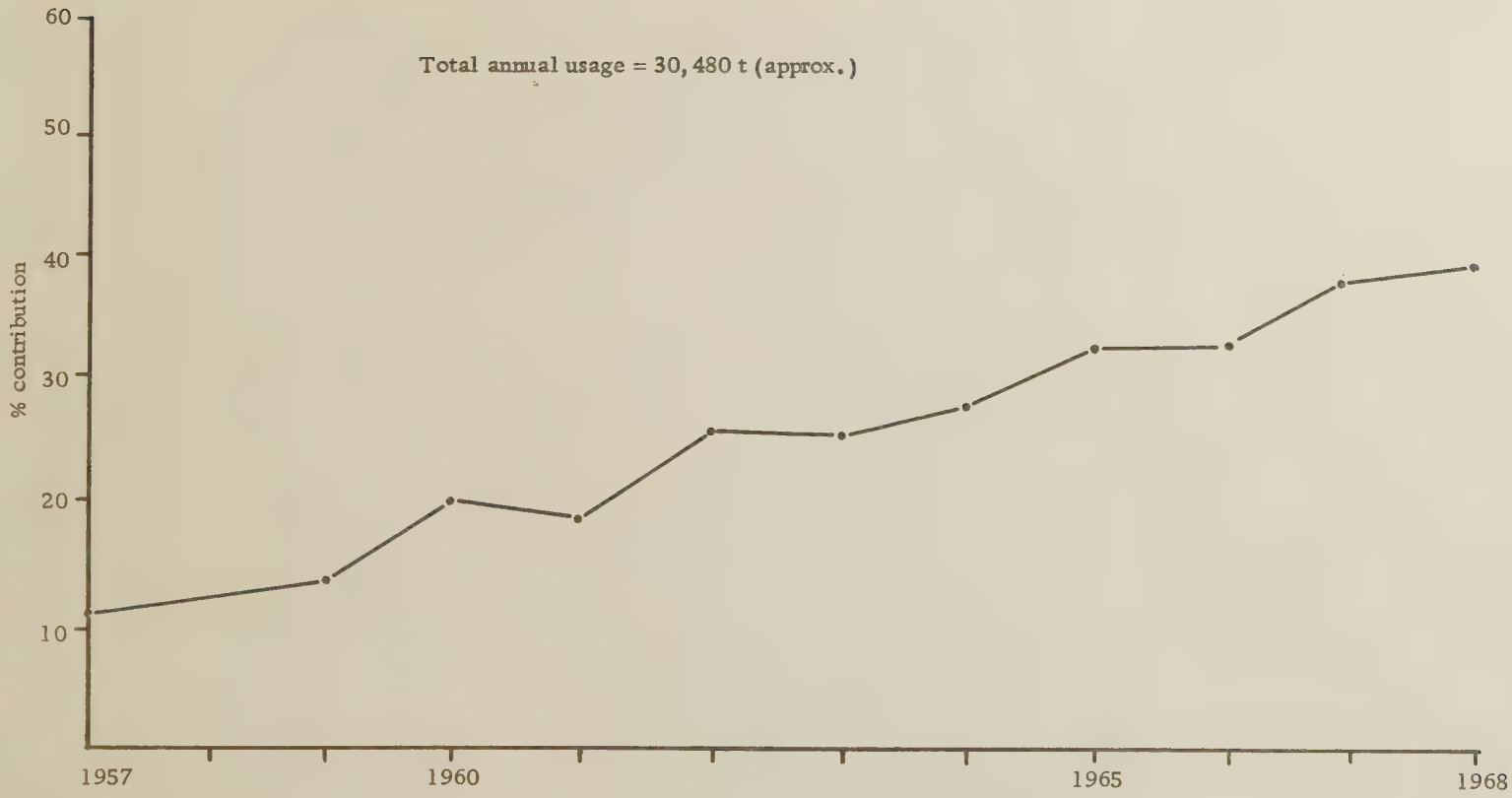


Fig.2. Percentage contribution of 'S' varieties to total usage of the five main grass species. 1957-1968.

The importance of herbage seed crop authentication had been realised in the very early years of the Station's history and from the outset it was considered essential to link production with an organized system of crop inspection in addition to a well controlled sequence of multiplication (5).

A Seed Crop Certification Scheme for its bred varieties of grasses and clovers was established by the Station in 1940 and for the first few years the whole of the inspection work was undertaken by the Station's staff. In later years this work was performed by Agricultural Advisory Officers who were given courses of training at Aberystwyth to qualify them for inspecting the seed crops on hebalf of the Station. This system continued until 1954 when responsibility for the administration of the Scheme was transferred to the National Institute of Agricultural Botany, Cambridge. In 1956 the National Scheme for Comprehensive Certification of Herbage Seeds was introduced through the formation of a National Certifying Authority for Herbage Seeds (N.I.A.B. S.P.Pub. No.4 - 1956) and as a result guaranteed seed of the Aberystwyth varieties became available to the farmer for the first time in sealed bags with labels carrying the certificate numbers and the trade mark of British Certified Seed.

Seed crops of 21 Station-bred varieties, representing nine species of herbage plants, are now being grown under the aegis of the Comprehensive Certification Scheme (see Herb. Breed. report).

Under the present scheme the Station produces regular quantities of Breeder's Seed of these varieties for the National Seed Development Organization (N.S.D.O.) which is, in turn, responsible for producing the next generation, the Basic Seed grade. The Basic Seed is distributed to seed firms for the production of Certified Seed under contract. All certified seed is thus only one generation removed from Basic Seed and not more than four generations removed from the individual plants which form the basis of the strain. The sequence of events in the multiplication process may thus be summarized as follows:

	Sequence of multiplication	
Responsibility of the Welsh Plant Breeding Station	Individual mother plants	= Basis of variety
	Vegetative multiplication	
	1st generation seed crop	
	Breeder's Seed	
Responsibility of the N.S.D.O.	Basic Seed	
Responsibility of the Seed Trade	Certified Seed	= Seed of commerce

The mother plants which form the basis of an individual grass variety are first of all vegetatively propagated and grouped together for mutual pollination at well isolated sites. The seed from these single plant polycross areas is cleaned and specially dried for long-term storage in moisture-proof containers at 0°C. This 1st generation seed (Syn I) is then used over a period of years to produce a further generation, namely Breeder's Seed. The scale of first generation multiplications depends upon several practical considerations, the most obvious of which are: potential demand, reproduction rates, and method of sowing (whether broadcast or in drills). Reproduction rates vary not only with the inherent reproductive capacity of a variety but also with the method used for multiplication. For example, cocksfoot grown for seed in wide drills at a seed rate of 5 kg/ha has a multiplication rate of 1:100, whereas broadcast crops of ryegrass sown at 15 kg/ha will produce a multiplication rate of only 1:33.

2. Arable crop varieties

The Department has been involved in the multiplication, maintenance and distribution of Breeder's and Basic Seed stocks (formerly known as Foundation stock) of a whole sequence of both winter and spring oat varieties developed by the Arable Crop Breeding Department. First came the pure line selections in the early 1930s derived from the old Welsh 'land' varieties and these together with two pure line selections from 'Hen Gymro' wheat comprised the first releases to a local Seed Growers' Association (Clarach Valley) which had been formed for the multiplication of these early stocks. In addition, the Station also introduced at the same time a cereal crop certification scheme for the authentication of these.

These pure line selections were soon replaced by winter and spring varieties which had been developed through hybridization, and increasing quantities of Basic Seed stocks had to be multiplied to meet demands. For this purpose the Station acquired in 1943 its 162 ha seed farm, Morfa Mawr, which is situated about 19 km south of Aberystwyth, and on which 80-100 t of Basic Seed of the Aberystwyth bred winter and spring oats are annually grown and distributed to growers and merchants for further multiplication in accordance with the requirements of the British Cereal Seed Scheme.

Current responsibilities comprise Breeder's and Basic Seed production of six oat varieties (three winter and three spring varieties) as well as a new winter rye variety for forage (Rheidol), a winter bean variety (Daffa) and a club root resistant forage rape (Nevin).

Nucleus stocks of the cereal varieties are produced in two stages. In the first year 1000 typical panicles are obtained from the breeders; these are each sown in 90 cm length of drill. To improve uniformity, all drills containing off-type progenies are discarded and the remaining rows are separately harvested. The produce of each row is sown in the following year as a two-row plot and before harvest each is again examined for uniformity, off-type progenies again being discarded. The whole area, which may extend to 1 ha, is then harvested in bulk to provide the Breeder's Seed stock for subsequent field scale production of Basic Seed.

Plate 1

First stage seed multiplication in pollen-proof compartments

Breeders seed crop of S.352 timothy

REVIEW OF HERBAGE SEED RESEARCH ACTIVITIES

The almost complete absence in England and Wales of experience in seed production of leafy grass varieties made investigations into the techniques of seed multiplication and into the maintenance of seed stocks matters of primary importance from the outset. As the varieties have been released for commercial production, seed firms, seed growers and advisory officers have looked to the Welsh Plant Breeding Station for guidance on basic cultural, manurial and management procedures for their field scale production so that an important part of the research programme has always been of necessity associated with production problems.

Initial techniques were based on the important researches undertaken by Gwilym Evans (3) who from his field experiments and experiences with the first field scale multiplications of the initial releases showed conclusively that the leafy varieties could be managed to produce satisfactory seed crops despite being bred exclusively for leafiness. As a result of continued research and application of developments in farm mechanization, fertilizer practices and chemical weed control, herbage seed production techniques have steadily improved since that time. Details of some of these aspects in which the Department has been concerned are briefly set out in the following pages together with an account of the more basic researches undertaken into inherent reproductive capacity, the physiology and biochemistry of flowering and seed formation. For convenience of presentation these are discussed under the following main subheadings namely (1) Seed production agronomy; (2) Seed harvesting, drying and storage; (3) Pollination studies; (4) Selection for improved seed productivity and seed retention; (5) Physiological and biochemical investigations.

1. Seed production agronomy

(i) Crop establishment

Of necessity the Department has conducted studies into the effects of drill width, seed rate and nurse crop upon the ultimate seed yielding potential of a crop.

The two chief methods of sowing grass seeds are: (a) in drills of 30 to 60 cm apart depending upon the variety, the number of crops to be taken, and the degree of inter-row cultivation intended, and (b) broadcast or in narrow drills. It was soon established that cocksfoot, timothy and tall fescue give their best results only when grown in drills, whereas perennial ryegrass, Italian ryegrass and meadow fescue give entirely satisfactory results when grown broadcast or in narrow drills. It was also found that, in general, the more leafy the varieties of cocksfoot or timothy, the less favourable are the seed yields from broadcast areas as compared with crops established in wide drills.

Initially, the standard width of drill normally recommended was 60 cm, but narrower drills such as 38, 45 or 53 cm have proved equally satisfactory. Only rarely have drill widths in excess of 60 cm given superior results. The results of experiments car-

ried out by Roberts (13) on S.37 cocksfoot, S.51 timothy and S.215 meadow fescue over three harvest years, serve to illustrate how yields are affected by drill widths. The four spacings used in these investigations were 15, 38, 60 and 90 cm.

Over three harvest years S.37 cocksfoot gave similar yields with drill spacings of 38 cm or more; narrower spacing had a deleterious effect. Drill spacing and N level showed a marked inverse relationship per unit seed production. With S.51 timothy the optimum drill width, consistent with maximum response to N, was found to be 60 cm, thus bearing out findings reported by Dutch workers. Meadow fescue gave the best yields with closer drill spacing (15 or 38 cm), thus resembling perennial ryegrass which performs best under broadcast or narrow drill conditions. Because of its relatively restricted root system, meadow fescue, like perennial ryegrass seems incapable of utilizing wider drill spacings as advantageously as either cocksfoot or timothy. A further practical disadvantage of growing the ryegrasses and meadow fescues in wider drill spacings is the proneness of the relatively short culms to lodge and for the heads to lie between the drills below the level of the cutter bar at harvest. Closer drills successfully overcome this difficulty and reduce the risks of loss through lodging. Sowing of both perennial and Italian ryegrass in narrow drills rather than broadcast results in better crop establishment and in fewer crop failures.

Seed rates: The conventional rates of seeding recommended for grass seed production are 4-6 kg/ha when drilled 36-60 cm apart and 8-15 kg when sown broadcast or in narrow drills. Like most other seed rate recommendations these were designed to be sufficiently flexible to allow for a range of seed bed conditions, for the varying drill widths adopted and general differences in seed size between species.

Investigations conducted at the Station into seed rates have indicated that, under good establishment conditions and with good control of weeds, lower rates can be used with advantage, particularly with the more extreme pasture types. For S.143 cocksfoot, S.48 timothy and S.170 tall fescue under wide drill conditions and adequate fertilizer applications a seed rate as low as 1 kg/ha has been found to give yields comparable with those obtained from 5 kg/ha seedings (Table 1).

In these investigations it was also found that spaced plantings gave even better yields. Under general farm conditions the extra cost involved in transplanting seedlings would not be justified, although the cross-gapping of established stands could well be considered on a farm scale as a means of reducing the excessive tiller numbers formed in older stands. High seed rates result in excessive numbers of plants and tillers endeavouring to establish themselves in the drills and competing amongst themselves for light, water and soil nutrients to the detriment of the optimum development of ear bearing tillers.

As in the case of wide drills, the evidence from both broadcast and close drilled crops shows that higher seed yields are obtained from light seed rates.

Table 1. Seed yields (kg/ha) derived from different seed rates for various harvest years (G. Evans 1959 and 1962)

Species and variety	Harvest year	Without spring N Seed rate per ha 1 kg	5 kg	With spring N Seed rate per ha 1 kg	5 kg
Cocksfoot S.143	1st	460*	367	820*	700
	2nd	247	168	343	343
	3rd	144	99	340	292
	4th	161*	106	247	200
Mean		253*	185	437*	389
Timothy S.48	1st	588	487	953*	694
	2nd	253	200	227	217
	3rd	172	144	156	159
	4th	184	192	283	296
Mean		299	256	405*	342
Tall fescue S.170	1st	-	-	211	217
	2nd	386*	253	520	422
	3rd	609*	490	501	505
Mean		498	372	340	309

* Denotes statistically significant (P = 0.05) differences from standard rate of 5 kg/ha

The use of low seed rates is of special interest to the Department in relation to the production of maximum quantities of early generation seed when seed stocks are the major limiting factors, and more recent investigations are thus concerned with the use of low seeding rates in conjunction with pre- and post-emergence sprays.

(ii) Fertilizer practices

The general principles of manuring for herbage seed crops were established in the early 1930s and these were based in the first instance upon the experiences gained by the seed growing industry in Denmark and Sweden. Early Station researches were thus concerned with establishing their soundness when applied to British conditions and to the production of seed from more leafy varieties.

There was an early appreciation of the basic importance of nitrogen for seed production. In consequence studies on grass seed crop manuring have tended to concentrate on the effects of nitrogen although at the same time there has been an appreciation of the need for a proper nutrient balance in the soil in terms of lime, phosphate and potash. Early experiments showed that little was gained in terms of increased seed yields from applications of these nutrients in excess of those required to make good the soil deficiencies, but these aspects are being looked at again with respect to

seed quality and effects on subsequent seedling and plant growth.

Initially, nitrogen is important in the establishment phase to ensure a sturdy and vigorous plant by the autumn, and in the first and subsequent harvest years further quantities are required, usually in spring, to maximize head production and head size. Exceptions to these general rules are the extra early flowering forms such as S.345 cocksfoot, S.170 tall fescue and S.59 red fescue which appear to benefit more from nitrogen applied in the preceding autumn rather than in spring.

Critical studies have shown that the plant is dependent on nitrogen supplies for all phases of development and that the amount available to the crop will determine the proportion of the tillers producing inflorescences. On the other hand, excess nitrogen can produce excess leafage and like cereals, such crops are prone to early lodging with consequent ill effects upon seed setting and development.

The time of application of nitrogenous fertilizer to grass seed crops in the spring is also an important factor and recent studies (11) have shown that the effects are related to the stage of growth of the crop at the time when nitrogen is applied. Nitrogen supplied some weeks before floral initiation produces its main effects by increasing the number of flowering shoots. Nitrogen applied during, or after differentiation of the apex contributes to yield by increasing individual head size, although in thin stands these later applications will also increase fertile tiller production. Such late applications will usually best benefit forward crops which have made vigorous growth during the early spring period. When N is applied to backward crops, heading tends to become uneven as a result of secondary tiller production and this in turn can often cause difficulties at harvest.

The requirements of the various Station bred grass varieties have been studied over many seasons and under varying management systems and for the benefit of growers, recommendations on dates and units of N to be applied have been prepared, based upon the results obtained (W.P.B.S.Technical Bulletin No.1, 1967). Of necessity, these recommendations have had to be highly arbitrary because of the other important interacting variables of soil type, spring temperatures, moisture and condition of crop.

In contrast to the grass seed crops, both red and white clover can produce excellent seed yields on land of only medium fertility and they have little need for application of nitrogen fertilizer because of their symbiotic N-fixing activities. Indeed, an application of nitrogen to a mixed white clover/ryegrass sward can cause a reduction in the number of clover blooms because of the increased growth of the grass component. However, both red and white clover require adequate amounts of lime, phosphate and potash in the soil and any deficiencies in these elements should always be rectified in the year of establishment. Further applications in the following spring are then considered unnecessary provided the crops have made normal establishment and growth and do not exhibit any deficiency symptoms.

(iii) Management studies

Work carried out in the course of the last twenty years at the Station has shown that management can exert a profound effect upon the seed yielding ability of crops. Emphasis has been placed on studies concerned with the effect of inter-row cultivation and defoliation on the seed yields.

Inter-row cultivations achieve the double objective of soil aeration and the reduction of weed and grass seedlings which establish in the inter-drill spaces. Most of the broad-leaved weeds, however, can now be effectively controlled by applications of one or more of the selective herbicides so that, in common with other row crops, the need for frequent cultivations has been greatly reduced. The elimination of the seedlings which establish in the inter-row spaces after harvest has still to be accomplished by cultivation, but weed and seedling control apart, it has been shown that early spring cultivations can impart beneficial effects upon seed yields. Late spring cultivations, on the other hand tend to depress seed productivity.

Herbage varieties vary greatly in the amount of foliage which can be removed without detriment to the seed crop. The research work undertaken on this subject also points clearly to the fact that the most important aspect of defoliation, performed either by grazing or by mechanical means, is the timing of the operation in relation to the stage of development of the crop (14, 15).

It has been established that both perennial and Italian ryegrass varieties respond favourably to autumn or early winter grazing, since it encourages the process of tillering and removes excess growth which is likely to suffer from winter burn and hamper early spring tiller formation. In contrast to cocksfoot, timothy, meadow and tall fescue, where the majority of the fertile tillers are autumn produced, the ear bearing tillers of both perennial and Italian ryegrass are largely developed in early spring, so that their removal has little effect on the seed crop. The beneficial effects derived from the autumn grazing of various perennial ryegrass varieties and the importance of timing if defoliated in spring are well illustrated by the results presented in Table 2.

These results and others have indicated that spring grazings tend to suppress yields unless the crop is supplied with adequate quantities of nitrogenous fertilizer and, especially so, if the defoliation is delayed beyond the date of ear initiation. Although, because of seasonal variations, no precise dates can be given by which spring grazing should cease, nevertheless results have shown that the critical stage to which spring grazings should be related is the date of inflorescence differentiation of individual varieties. This means that the later flowering varieties such as S.23 or S.101 can be grazed later than S.24.

Basically, Italian ryegrass is similar to perennial ryegrass in its sensitivity to defoliation, but a fairly late grazing is beneficial in helping to avoid early lodging of the crop.

Table 2. The combined effect of grazing and manuring perennial ryegrass varieties at different times of the year

	Seed yields (kg/ha) obtained from the different varieties											
	S.24			S.321			S.23			Melle Pasture		
	N_1	N_2	N_3	N_1	N_2	N_3	N_1	N_2	N_3	N_1	N_2	N_3
Ungrazed (control)	462	633	595	719	901	981	262	370	434	283	431	574
Autumn-grazed end of September	618	754	695	905	1029	1182	419	533	621	402	608	687
*Spring-grazed at ear formation (a)	430	471	541	562	716	743	313	400	480	298	409	594
Spring-grazed 3 weeks after ear formation (b)	431	450	511	652	787	765	297	302	320	416	405	475

*Spring grazing treatment related to date of ear formation

Manurial treatments: N_1 = 105 units N per hectare
N_2 = 210 units N per hectare
N_3 = 315 units N per hectare

		(a)	(b)
Actual dates:	S.24 =	1 April	22 April
	S.321 =	9 April	30 April
	S.23 =	22 April	13 May
	Melle =	12 April	3 May

Grazing treatment L.S.D. value at P = 0.01 = 104.8
Nitrogen treatment L.S.D. value at P = 0.01 = 58.5

Because of its slower rate of establishment, drilled crops of cocksfoot sown in a cereal crop rarely require grazing in the first autumn, but forward stands resulting from direct sowings can be grazed or topped over without detriment to the ultimate seed yield. Experimental data have indicated that spring grazing should not be continued beyond the inflorescence initiation, which occurs around mid-March in S.26, S.37 and S.143. The very early differentiation which characterizes S.345 precludes the imposition of any spring defoliation in the case of this variety.

The bred varieties of timothy respond to autumn and winter grazing in the same way as cocksfoot, and lenient defoliation can be practised in the October to December period without adverse effects. The fact that timothy varieties, as a group, initiate inflorescences 2 to 3 weeks later than cocksfoot means that they can withstand slightly later spring grazings. If, however, an early April defoliation is followed by a period of dry weather a reduction in yield can occur.

Improved seed yields are a general consequence of late autumn or early winter defoliation in the meadow fescue varieties S.53 and S.215 and also in tall fescue S.170. Spring grazing undertaken after inflorescence formation will markedly depress yields.

White and red clover seed crops benefit from defoliation in different ways. Grazing has several roles to play in white clover seed production, for defoliation of the crop up to the early bud stage encourages stolon development, preserves soil moisture and, most important, reduces the shading effect of leaves at the critical stage when environmental conditions are approaching the optimum for flower formation.

With red clover the annual practice is to cut for silage or graze up to the end of May and then to take seed from the aftermath. In view of the risks involved in red clover seed production, this method has obvious economic advantages. Experimental observations on S.123 red clover in both dry and wet seasons gave a clear indication that higher seed yields can be obtained from crops which are not defoliated or are cut at a height of 10 cm. The excessive leafiness normally associated with maiden crops can now be effectively controlled by the use of pre-harvest desiccants and it may be that the key to future yield increases in red clover lies in this direction.

(iv) Chemical weed control

Experimental work conducted by the Department on chemical weed control in herbage seed crops has been mainly concerned with the establishment of weed-free experimental plots and this has included the use of chemicals as pre- and post-emergence sprays. The effectiveness of the techniques has been demonstrated by the fact that, amongst other grasses, meadow fescue, a species which tends to be low in its competitiveness with weeds, has been maintained in a weed-free condition in both drill and broadcast plots over several harvest years.

Techniques have been developed for the direct sowing of grass and clover seeds in seed beds prepared some 10-14 days previously. A complete kill of seedlings established from the indigenous buried weed population is achieved through the application of

paraquat or PCP either immediately before seed sowing or immediately after sowing, but before the crop seedlings have emerged. The effectiveness of this method in reducing weed cover and in encouraging crop growth is well illustrated below:

Growth of S.215 meadow fescue in relation to seed cover after spraying with PCP (after Lewis, 1969)

Treatment	% weed cover 2 months after harvest	Tillers/plant	Wt (g) per 100 plants	Wt (g) per 100 tillers
Pre-emergence PCP	17.5	2.30	19.9	8.68
Untreated control	70.0	1.75	7.7	4.42

After establishment it has been found that the broad leaved weeds which appear at the later stages of crop growth can be controlled by means of a spring spraying programme involving hormonal sprays such as M. C. P. A., M.C.P.B. or 2,4-D which should be completed not later than 4-5 weeks before the expected date of ear emergence.

2. Seed drying and storage

The care of seeds after harvesting has, of necessity, formed an integral part of the Department's research programme since its inception. Investigations have been concerned with the post harvest conditioning of seeds as well as the determination of the optimum conditions for both short and long term storage of seed stocks.

(i) Seed drying

The germination capacity of freshly combined seed of high moisture content may be destroyed very rapidly if the crop is left in sacks or bins without artificial drying. It is considered safe for seed to remain in bulk after threshing only if the moisture level is below 14% and even then, because of the leaf and stem debris usually found amongst threshed seed, either spreading out or artificial drying may still be needed.

There are two types of moisture involved in seed conditioning; moisture occurring on the outer surface which the air readily absorbs under dry atmospheric conditions, and internal moisture which is distributed throughout the inner parts of the seeds. Early research established the principle, that the higher the moisture contained in the seed, the lower must be the drying temperature used in the drying process and consequently the longer the time needed to reach the desired dry condition. Subsequent investigations with other species have confirmed these earlier findings and for practical purposes drying temperatures in the 32-43°C range are now regarded as optimal temperatures for grass seed with a moisture content in excess of 20%. Under no circumstances, however, should the temperature of the drying air exceed 49°C, even for reasonably dry seed, because of the risk of affecting germination capacity.

(ii) Seed storage

Continued drying and storage experiments undertaken in the Department have indicated that grass seeds dried to moisture levels of 13-14% can be stored satisfactorily in bulk over a 12-month period under ordinary unheated warehouse conditions. Optimal moisture levels have been shown to vary slightly with species, those established for ryegrass, cocksfoot and timothy being 14.0%, 13.0% and 13.5%, respectively. However, with extended storage, the problem is not only one of initial drying to prevent overheating or mouldiness, but also of slowing down the overall respiration rate of the seed to conserve viability, an aspect which also involves conditions of storage.

Information has been obtained on moisture levels, conditions of storage and type of containers best suited to maintain viability over varying periods of time. For instance, it has been established that the germination of certain grasses, e.g. meadow fescue seed, can be effectively maintained over a 3-year period under ordinary unheated warehouse conditions only by drying to below 10% moisture content and storing the seed in moisture-proof bags or in sealed containers. Most grass and clover seeds can be successfully stored in this way, but if storage periods of longer duration are contemplated, viability can only be ensured by maintaining constant low temperature storage conditions of around 0°C. The effectiveness of low temperature in maintaining viability over a long term is well illustrated by the results obtained by Roberts (12) for meadow fescue and timothy seed.

Table 3. The effects of different moisture levels and storage conditions on seed viability in meadow fescue and timothy over 11 years

		Meadow fescue (orig. germ. = 96%)			Timothy		
	Period of storage	Orig. % moisture levels			Orig. % moisture levels		
Storage	(years)	16.6	11.8	8.9	13.5	11.7	7.7
Cold storage	1	93	95	90	98	98	98
	2	91	95	97	98	98	98
	3	91	95	93	98	97	97
	11	79	95	90	96	97	96
Laboratory	1	79	93	95	92	95	97
	2	58	88	91	82	91	91
	3	45	81	86	80	90	91
	11	0	0	1	0	2	2
Warehouse	1	72	88	96	94	97	97
	2	14	75	86	56	86	95
	3	3	50	77	33	67	73
	11	0	0	0	0	0	0

(iii) Effects of storage on subsequent plant growth

Apart from viability, the other obvious concern of seedsmen and plant breeders with drying and long term storage is the effect of these processes on subsequent plant growth, reproduction, and ultimate effects on the offspring of the plants. Various seed lots of S.23 perennial ryegrass, artificially dried to very low moisutre levels, ranging from 5.5% to below 1.0%, and stored for a 20 year period, have been tested at regular intervals for germinating capacity, and the effect of the long term storage on subsequent plant development was studied.

Observations on mature plants derived from seed lots stored for 20 years revealed no real difference in the general growth habit in comparison with plants derived from yearling S.23 perennial ryegrass seed. Pollen fertility, however, was reduced in 38% of all the plants studied, and the seed setting capacity was affected to an even greater extent, with 44% of the plants giving seed set values well below those obtained for plants grown from new seed. Reduced pollen fertility was usually associated with low seed setting, but there were instances of satisfactory pollen fertility associated with a low seed set (8).

Present investigations are concerned with the next generation and with determining the satisfactory nature, or otherwise, of their progenies. Preliminary results indicate that the type of plant was not in any way affected and, in addition, that fertility has been largely recovered, indicating that neither the long term storage period nor the processes of drying have in any way altered the genetical constitution of the variety.

3. Pollination studies

The forage grasses and clovers in widespread use are naturally cross-pollinated and for all practical purposes may be considered self sterile. The danger of serious contamination of seed stocks during multiplication is, therefore, always present if exposure to compatible 'foreign' pollen occurs. Proper isolation standards are consequently of paramount importance in maintaining the genetic purity of improved varieties.

Cross pollination in the grasses and clovers is effected, respectively, through the agency of wind and insects. Isolation requirements for clovers are intimately connected with the foraging behaviour of bees, who are the principle agents of pollination. Likewise, in dealing with the wind pollinated grasses, atmospheric turbulences, wind direction and speed, height of crop and the buoyancy of pollen are all factors concerned in contamination.

The synthesis by Station breeders of non-red-base perennial ryegrass populations and clover strains characterized by the absence of leaf markings facilitated critical studies on natural outcrossing in perennial and Italian ryegrass (7) red clover (22) and white clover (16). Results obtained from the ryegrass investigations have provided information on how isolation requirements may be fulfilled by distance, border drills

or a combination of these methods. These results emphasized the importance of making initial multiplication areas as large as possible, because the quantity of pollen produced within multiplication plots is as important in its effects as isolation distance. It has been clearly established that the smaller the exposed plot in relation to the contaminant, the greater the risk of crossing.

Both size of plot and abundance of blooms were found to be of great importance in relation to the amount of out-crossing noted in the clovers and, indeed, it was concluded from the results that the purity of a legume seed crop is more dependent upon the abundance of blooms within the crop than upon the distance separating it from other crops.

More recently, investigations have been concerned with estimating the extent to which cross fertilization can occur between diploid and tetraploid ryegrass varieties grown close together, between tetraploid ryegrass and tall fescue, and between tetraploid ryegrass and the amphiploid derived from the cross Italian ryegrass x tall fescue.

The results, obtained from the studies undertaken to determine the degree to which diploid and tetraploid ryegrass varieties intercross under field conditions, indicate that pollen from tetraploid ryegrass constitutes little or no danger to the genetic purity of diploid seed crops, even if grown in close proximity. A small proportion of viable triploid hybrids can arise in the progenies of tetraploid plants heavily exposed to diploid pollen, but here again their frequency and incidence are of no practical consequence (9). More detailed crossing experiments, however, have shown that the incidence of crossing is greater than that indicated by the frequency of derived hybrids. When crossed under controlled conditions, the diploid x tetraploid crosses and their reciprocals gave seed set values approaching those of the diploid x diploid and tetraploid x tetraploid control crosses, but the majority of seed were poorly developed and failed to germinate. Embryo culture showed, however, that large numbers of triploid hybrids could be cultured from embryos dissected from 12-day old seeds. These were cultured firstly in artificial media and then successfully transplanted to develop into fully grown plants.

4. Selection for improved seed productivity and seed retention

Although much has been accomplished towards obtaining reasonable seed yields from the pasture varieties through the development of specialized cultural, manurial and management techniques, experience with the extreme pasture forms has shown that their seed potential is generally lower than that of some other commercial varieties. Therefore it was decided to investigate whether the existing seed yielding potential of a number of the bred varieties could be improved through further reselection without detriment to the forage producing qualities. This work was first initiated in the early 1960s to investigate the variation in the seed production characters of S.53 and S.215 meadow fescue, S.170 tall fescue, S.48 timothy and S.23 perennial ryegrass. Factors which contribute directly towards seed yield, as well as those which indirectly influence or limit yield, have been taken into consideration.

Table 4. Improvements achieved in the seed producing characteristics of S.170 tall fescue and S.48 timothy (E.W.Bean - unpublished data)

	Seed yield per plant (g)	Inflorescence number	Seed weight per inflorescence (g)	Florets per inflorescence	Fertility	1000 seed weight (g)
S.170 tall fescue						
Mean of 49 genotypes	31.8	92	0.35	278	50.0	2.52
Mean of 6 selected genotypes	49.0	98	0.50	336	57.0	2.63
% increase	54.0	6.5	42.0	20.8	14.0	4.4
S.48 timothy						
A. Mean of 49 genotypes	36.4	211	0.20	-	-	0.43
B. Mean of 6 selected genotypes	54.6	222	0.28	-	-	0.46
% increase B over A	51.0	5.0	40.0	-	-	7.0

(i) Factors contributing directly to seed yield in grasses

The basic factors are (1) the number of inflorescences produced per plant, (2) the number of florets produced per inflorescence (head size), (3) the proportion of florets which set seed (seed setting ability), and (4) individual seed weight.

All these components are highly influenced by environmental factors, nevertheless the investigations have shown considerable heritable variation. The heritability values obtained in respect of these components have also indicated that a positive and rapid response to selection should be possible without undesirable effects on varietal vegetative characteristics. An indication of the improvements possible in seed yield potential through a study of the seed setting characteristics of the inflorescence is well illustrated by the results obtained by E. W. Bean (unpublished) in his investigations with S.170 tall fescue and S.48 timothy which are reproduced in Table 4. Table 4 shows that in both S.170 tall fescue and S.48 timothy the increase of seed yield of 54% and 51% respectively was obtained by increasing the mean seed yield per inflorescence (42% and 40% respectively), while the inflorescence number was only marginally increased.

Experimental populations based on plants selected by adopting similar procedures have already been established from S.215 and S.53 meadow fescue and included in seed yield tests to determine the extent of the actual advance made on the basic varieties. The results obtained from a comparison of first generation seed stocks over two harvest years together with one year's harvest result for a new S.23 reselection, are reproduced below:

Table 5. Relative advances made in the seed producing characteristics of S.215 and S.53 meadow fescue and S.23 perennial ryegrass (Lewis- unpublished data)

Variety	Harvest year	Seed yield (kg/ha) Standard variety	New selection	Mean % improvement
S.215	1st (1965)	544	722	19.7
	2nd (1966)	772	854	
S.53	1st (1965)	420	379	13.1
	2nd (1966)	396	544	
S.23	1st (1968)	1048	1228	17.2

In all these selection programmes the flowering dates of the new material are the same as those of the original varieties. Preliminary tests with the meadow fescue selections have indicated that the improved selection lines are comparable in forage production with the original populations.

(ii) Indirect limiting factors

In addition to the factors which contribute directly to seed productivity, reselection

can also provide the means of improving traits which limit yield indirectly, e.g. an unusually extended spread in flowering time and maturity, excessive proneness to lodging prior to pollination, proneness to seed shattering and disease susceptibility.

The necessity for a close matching of the basic clones for time of flowering is well recognized as a pre-requisite for maximum yields and for preventing genetic shift.

Considerable variation in proneness to lodging has been observed in meadow fescue, timothy, tall fescue and perennial ryegrass species. Whilst it is agreed that ultimate lodging is decidedly advantageous for the avoidance of seed shattering at harvest, in early lodged crops pollen has little opportunity for dispersal, especially in damp weather, with the result that the lower-most inflorescences will have in no way achieved their seed setting potential.

Like lodging resistance, seed retention is a character which is not highly developed in grasses, and losses incurred through shattering can be very substantial, often in the range of 30-40%, representing the difference between profitable and indifferent yields.

In his investigations with S.48 and S.51 timothy, Bean (1) has found that individual clones varied in two respects; their capacity to retain their spikelets in the field, and the ease with which seeds separate from their ensheathing glumes during the process of threshing. What is required in timothy are heads which do not readily strip in the field with the approach of maturity, yet at the same time make possible the ready separation of the seed from the glumes in the threshing process.

Disease has also been noted to be a major cause of poor seed setting in S.345 cocksfoot. As a result of severe infections of the main culms and inflorescence branches by Selenophoma donacis the seeds fail to fill properly and in many instances whole inflorescences shrivel up completely long before the normal time of maturity.

This was first of all noted in 1966 when a considerable proportion of the plants under study developed large necrotic lesions on their culms. The plants were scored on a 0-5 scale for severity of attack and, at maturity, heads were taken from some of the slightly infected (rated 0, 1 and 2), and from the heavily infected plants (rated 4 and 5) for a seed fertility analysis, and the results showed a mean seed set of 32.0% for the slightly infected plants and 0.04% for the heavily infected.

The above results show a strong relationship between seed set and the degree of infection, and in particular, the degree of necrosis which was evident on the culms and inflorescences. These studies also revealed the occurrence of resistance within the variety and there is every promise of developing a resistant selection to replace the original stock.

5. Physiological and biochemical investigations

Investigations into the physiology and biochemistry of flowering and seed formation

in the grasses and clovers date approximately from 1965 and are, therefore, a comparatively recent activity of the Department.

(i) Induction requirements in the genus Festuca

Whilst the requirements of the other important genera (Dactylis, Lolium and Phleum) have been examined in detail by J.P.Cooper and his colleagues the requirements for inflorescence production in the genus Festuca have been recently studied in this Department.

Information obtained to date by E.W.Bean (2) suggests that F. arundinacea and F. pratensis have a juvenile stage of about four weeks duration when the seedlings show no response to daylength or low temperatures. After completion of the juvenile phase, induction proceeds most rapidly under natural conditions of short days and low temperatures. The period required to complete induction varied widely between genotypes of F. arundinacea, but all plants are fully induced by the end of December. The initiation of reproductive primordia then proceeds in the comparatively short daylengths of January and February. Initiation can be observed in the field at the beginning of February in F. arundinacea and F. rubra and at the end of March in F. pratensis.

An investigation to determine the reasons for the low frequency of inflorescence production when the amphiploid derived from the cross L. multiflorum x F. arundinacea was grown in drills, showed that the inductive requirements of the hybrid were intermediate between those of the parents, and that tillers could become induced under field conditions. The possibility therefore existed that the competitive effects operative in the drill were preventing the normal change-over from vegetative to reproductive growth. This contention was supported by the finding that nitrogen applications increased the number of inflorescences produced.

Future studies will be concerned with determining the optimum conditions of daylength and temperature for induction in the Festucae in order to reduce the generation interval to the minimum.

(ii) Red clover gibberellin studies

The early studies on flowering undertaken by J.L.Stoddart from 1956 to 1959 were centred upon the feasibility of altering the flowering behaviour of Station bred late-flowering varieties. Difficulty was being experienced in producing the quantities of seed of S.123 and S.151 required to meet commercial needs principally because these selections normally set seed late in the season when the risk of unfavourable ripening conditions is highest.

The initial physiological approach was concerned with the elucidation of the factors controlling the onset of stem elongation and flowering together with an assessment of the correctness of the prevailing seed crop management practices. At this time

some of the more spectacular plant hormones, such as gibberellic acid, were just becoming generally available for experimental purposes and in the course of a screening programme it was noted that some of them produced effects which might be used to advantage in the red clover seed production. Gibberellic acid was found to accelerate emergence in S.123 by as much as 10 days without any apparent effects on the number or size of blooms produced, whilst TIBA (2,3,5, Tri-iodo benzoic acid) gave a marked reduction in apical dominance at an early stage in the stem elongation phase, resulting in a compression of the period during which flowering emergence occurred (17).

Unfortunately, many of the benefits of such chemical treatments were more than outweighed by undesirable side-effects. Gibberellin tended to produce excessively long stems and, therefore, a substantially increased risk of lodging. The effective concentration range of TIBA was so narrow that field-scale treatment became extremely complicated. Notwithstanding these objections, the gibberellin response provided a method of reducing generation time in red clover, potentially useful in situations where lodging could be controlled, e.g. in glasshouse breeding programmes. The early gibberellin work also brought to light many of the physiological problems which have formed the basis of more recent studies.

For example, at an early stage in studies concerned with changes in the endogenous gibberellin contents of early and late flowering varieties of red clover, it was found that the extracts frequently contained more than one type of gibberellin and that the quantitative and qualitative composition of the extracts varied both with variety and photoperiod. By choosing suitable concentrations and treatment stages it was possible to use gibberellin to effectively remove the phenotypic differences between early and late flowering cultivars, thus demonstrating the key position held by this group of hormones in the genetic expression of species differences (18). Furthermore, it was seen that the appearance of one of the gibberellin components could be closely correlated with the transition of the shoot apex from the vegetative to the flowering condition. Subsequent studies showed that the relationship was an indirect one, a conclusion reached principally with the aid of non-flowering mutant genotypes of red clover.

These genotypes were produced by recurrent selection for lateness within a late-flowering population and remained vegetative under normally flower-inducing environmental conditions. Assays showed that the endogenous gibberellin content of this material was reduced in comparison with normal plants under the same daylength conditions and it was found that supplementation of the gibberellin level by means of spray treatments resulted in an essentially normal stem extension and flowering behaviour. Studies of the partial processes involved revealed that two separate systems were recognizable, one concerned with the perception of the inductive photoperiod and the other involved in the expression of the floral stimulus. It was found that free gibberellin was required for the second process, and it was also shown that plants needed to exceed a specific threshold of free gibberellin content before they could successfully complete the processes of floral induction.

In more recent years, the control mechanisms limiting gibberellin synthesis have

received a great deal of attention. The multiple gibberellins occurring in clover leaf extracts have been shown to be parts of a metabolic sequence which contains at least one step with an absolute light-dependence. This system, therefore, contains a possible means whereby the regulation of hormone synthesis by external factors could be achieved. Some attention has also been paid to the location of the sites of gibberellin synthesis within the leaf, and recently it was discovered that a significant proportion of the total hormone in the leaf could be located within the chloroplast. Studies have now shown that the plastid membrane is permeable to gibberellin and that this organelle could, therefore, be the source of most of the leaf activity. Parallel studies, carried out in collaboration with the Developmental Genetics Department have also indicated that the activity of the primary carboxylating enzyme in the photosynthetic pathway is greatly affected by increases in leaf gibberellin level.

(iii) Seed development studies

The study of seed development was initiated because of the highly variable seed yields obtained from the grass varieties from one season to another. It was suspected that the problem would be compound in nature, stemming partly from inherent deficiencies in the seed setting and seed forming capabilities of the varieties themselves, and partly from inconsistencies or inaccuracies in the management regime applied. The period 1956-1958 was largely occupied with attempts to influence the course of seed-shedding from the inflorescence by means of synthetic auxin treatments. This approach was based upon an analogy with the situation in fruit crops, where it was shown that the abscission of the fruit appeared to depend upon the auxin gradient across the peduncle. Although some limited success was obtained in the case of Phleum and Phalaris, it was quickly realised that economic considerations were greatly in favour of breeding for increased seed-retentivity.

An early outcome of this work, however, was that there did not seem to be any accurate or generally applicable descriptions of the state of ripeness in seeds of the various grass species in common agricultural use. Therefore, a large proportion of the research time undertaken by J.L.Stoddart between 1960 and 1965 was devoted to the compilation of detailed physiological and biochemical pictures of the ripening process in seeds of all the major grass genera (19, 20, 21). Trends in major metabolites were then related to morphological changes in the seed and these were, in turn, used to construct criteria upon which ripeness assessments could be based.

In general, all varieties showed a unified relationship between the metabolite patterns and changes in such factors as endosperm consistency and seed moisture content. Unfortunately, seed colour, the most frequently used field ripeness criterion, proved not to have any strict relationship with the stage of ripeness of the seed. On the other hand, it was found that some ryegrasses (notably S.321) produced anthocyanin in the seed epidermis immediately upon attaining physiological ripeness thus provided a very accurate indication of the earliest safe harvest point.

Many of the metabolic conversions occurring during the second half of the seed

ripening were found to proceed at an undiminished rate in culms severed from the root system, and in 1964-65 attempts were made to estimate the exact point at which the seed development sequence became independent of the parent plant. It was found that seed severed after the maximum free sugar content had been attained could complete the full ripening sequence. Earlier harvests usually resulted in decreased final seed weights and reduced vigour of progeny. Varietal differences in this effect were, however, evident (Plate 2). This finding aroused interest in the systems controlling seed formation and an active programme on this aspect is being pursued at present.

Seeds are a par excellence source of gibberellin and in this respect grasses are no exception, building up a peak seed content which is at least 100 times greater than the level found in any other plant at any time. The maximum coincides with the period during which the initial rapid seed expansion occurs and it is tempting to argue that the gibberellins act as seed setting factors. This idea is even more attractive in situations such as that in Phleum where the seed gibberellin is different from that characterizing the inflorescence before anthesis. Current studies also indicate that some of the key enzymes required for endosperm formation are sensitive to gibberellin level and, therefore, open to manipulation.

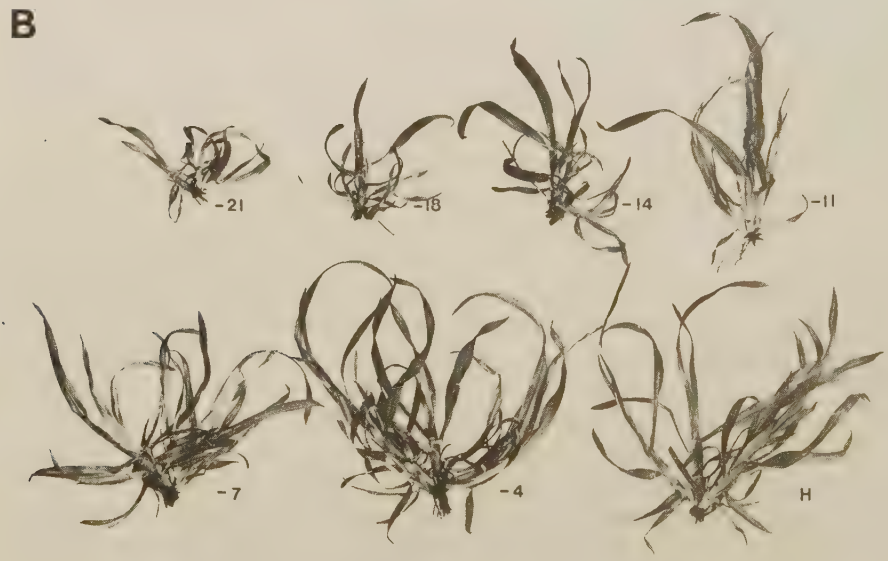
(iv) Effects of growth retardants on grass seed crops

Quarternary ammonium growth retardants, such as CCC, have been arousing interest since about 1964 and they are now in extensive use in Austria and Germany for the reduction of lodging in cereal crops. During this period, evaluation trials were carried out in the Department with somewhat mixed results. The Station timothy varieties were all found to respond to the chemical, and culm length reductions of up to 30% were regularly obtained, but fescues in general gave no response whatsoever even at very high dosage rates. In some genera, therefore, CCC may be regarded as a potential aid to seed production. It was generally believed that this group of compounds exerted their effects on the plant by means of a specific blockage of the gibberellin biosynthetic pathway, but present opinion tends to favour a broader spectrum of action. One of the first indications that this might be so was the finding in the Department that the chemical composition of the grass plant is radically altered within hours after treatment and that many of the effects observed cannot be explained simply in terms of reduced gibberellin synthesis.

(v) Biochemical aspects of host-parasite reactions

Because one of the inevitable results of most plant diseases is a reduction in seed yield, an extensive collaboration has built up over the years between the Herbage Seed Research and Plant Pathology Departments. Joint publications have been produced on white clover phyllody and Verticillium wilt. Phyllody, or 'green-petal' virus was shown to produce abnormal auxin levels in the developing inflorescence bud, and it was found that these effects could be overcome by raising the zinc level of the soil or solution in which the plants were growing. This treatment allowed normal inflorescences to be formed in the presence of the virus and provided a possible method for

Plate 2. Effect of harvest date on seedling vigour in S.321 perennial ryegrass and S.143 cocksfoot



A. S.321 perennial ryegrass; B. S.143 cocksfoot
Month-old seedlings derived from seeds harvested at various stages of maturation.
H = Harvest point, as determined by conventional field-scale criteria. Other dates are expressed as days prior to this point (e.g. -3 means, harvested 3 days earlier than H).

ameliorating the effects of the virus on a field, or glasshouse, scale.

The chemical nature of the toxin produced by Verticillium albo-atrum, the causal agent of lucerne wilt, has been elucidated. Most of the wilt activity was found to be associated with a high molecular weight glyco-protein, which is thought to interfere with cell permeability.

FUTURE RESEARCH ACTIVITIES

Studies on the controlling factors involved in the onset of reproductive growth in herbage species are in an early stage, and projects aimed at a fuller understanding of these processes will clearly play a large part in future research activities. Advances in this area would allow the timing and rate of flower formation to be manipulated, thus providing the seed grower with a greater degree of control over the seed crop. Such knowledge would also facilitate the development of non-flowering grasses.

The control mechanisms underlying seed development will continue to be studied, with the ultimate objective of devising methods whereby the rate of ripening could be influenced on a field scale. Such studies also hold the possibility of development of techniques enabling seed viability to be maintained without recourse to expensive low-temperature storage facilities.

Environmental effects upon seed setting are poorly understood and the possibility of seed of Station varieties being grown abroad makes it imperative that more accurate information should be available on the influence of climatic variations on the development and quality of seeds. Seed quality has recently assumed importance with the realization that the establishment of the subsequent crop is influenced to a significant degree by, as yet, undefined qualitative characteristics of the seed. Research in this area will clearly pay dividends.

Investigations will continue into the possibilities of selection for seed-producing characters. Components of yield which are not correlated with deleterious effects upon herbage production will be sought and developed to the point where they can be incorporated by the breeder into future releases.

Similarly, it is desirable to continue efforts towards the production of hybrid cereal and herbage varieties and, in this context, it is important for us to increase our knowledge of the factors involved in the control of male sterility.

As in the past, the Department will constantly seek to adapt, refine and utilize new techniques in the fields of management, crop cleanliness and mechanical handling with the aim of a steady progress in the efficiency of crop scale seed production.

References

(1) E.W.Bean, 1965, J.Br.Grassld Soc. 20, 144-147.
(2) E.W.Bean, 1970, Ann.Bot.N.S. 34, 57-66.

(3) G. Evans, 1937, Bull. Bur. Pl. Genet., Aberystwyth, 22, pp.36.
(4) G. Evans, 1959, Emp. J. exp. Agric. 27, 291-299.
(5) G. Evans, 1961, Welsh Pl. Breed. Stn Report for 1960, 82-93.
(6) G. Evans, 1962, Emp. J. exp. Agric. 30, 181-191.
(7) D. J. Griffiths, 1950, J. agric. Sci., Camb. 40, 19-38.
(8) D. J. Griffiths and R. A. D. Pegler, 1964, J. Br. Grassld Soc. 19, 183-190.
(9) D. J. Griffiths and R. A. D. Pegler, 1966, J. Br. Grassld Soc. 21, 162-166.
(10) J. Lewis, 1964, 7th Br. Weed Control Conf. p.367-371.
(11) J. Lewis, 1968, J. Br. Grassld Soc. 23, 240-246.
(12) H. M. Roberts, 1959, Proc. Int. Seed Test. Assoc. 24, 184-213.
(13) H. M. Roberts, 1961, J. Br. Grassld Soc. 16, 37-42.
(14) H. M. Roberts, 1965, J. Br. Grassld Soc. 20, 283-289.
(15) H. M. Roberts, 1966, J. agric. Sci., Camb. 66, 225-232.
(16) H. M. Roberts, 1967, Welsh Pl. Breed. Stn Report for 1966, 103-105.
(17) J. L. Stoddart, 1961, Ph. D. Thesis, Univ. College of Wales, Aberystwyth (unpublished).
(18) J. L. Stoddart, 1963, Nature, Lond. 199, 1270-1271.
(19) J. L. Stoddart, 1964a, J. agric. Sci., Camb. 62, 67-72.
(20) J. L. Stoddart, 1964b, J. agric. Sci., Camb. 62, 321-325.
(21) J. L. Stoddart, 1964c, J. agric. Sci., Camb. 63, 397-402.
(22) R. D. Williams and G. Evans, 1935, Welsh Jour. Agric. XI, 164-171.

ARABLE CROP BREEDING

J.D.HAYES

The main functions of the Arable Crop Breeding Department are to breed improved varieties of those arable crops which are of major importance in western Britain, and to conduct research investigations which will provide information leading to refinements in breeding procedures and to further advances in varietal performance.

This combination of breeding and research has existed from the time of the inception of the Station, but over the years the emphasis on various crops and problems has changed in response to the changing agricultural situation and research needs.

During the first half of the period from the founding of the Station until the present day, most of the work was concentrated on oats. With the limited facilities and staff available for cereal investigations, E.T.Jones was well justified in confining his attention to oats, since at that time it was the most important cereal crop in the United Kingdom. Both the grain and straw provided valuable animal feed, and it was well suited to the existing agricultural practice. The land generally, and in particular in the west of Britain, had a low pH which was better tolerated by oats than by the other cereals. However, the second World War gave great impetus to arable crop production in the west of Britain. The increased use of fertilizers and lime, the introduction of short-stiff-strawed high yielding varieties of spring barley, and the superseding of the binder by the combine harvester, all contributed to a gradual displacement of oats by barley.

Under the leadership of D. J. Griffiths, the Department was considerably expanded during the early and middle fifties, and with the increased staff facilities the scope of the breeding and research investigations was increased and extended to barley, field beans and the brassica crops. With the intensification of cereal production it soon became evident that disease susceptibility was of overriding importance in preventing the realization of the full yield potential, and therefore the staff and facilities of the Station were again expanded to promote understanding of disease resistance and to develop resistant genotypes.

REVIEW OF BREEDING ACHIEVEMENTS IN CEREALS

The early oat breeding work was concerned with increasing grain yield and improving grain and straw quality by developing varieties adapted to specific environments.

In more recent years there has been increased emphasis on the development of widely adapted varieties suited to mechanized harvesting and able to exploit high levels of fertility.

Amongst the winter oat varieties produced by E. T. Jones, who was in charge of the work of the Department until his appointment as Director in 1950, special mention should be made of the following varieties, as each marked a significant step forward in making oats competitive with the other cereals. S.147, released in 1938, was the first winter variety to combine high quality grain with good yielding ability and straw of moderate length and strength. It was followed in 1939 by S.172 with very short stiff straw which facilitated the growing of oats under very much higher fertility conditions than had previously been possible. Because of the extreme stiffness and shortness of their straw, S.172 and the spring variety Milford (S.225) derived from a cross of S.172 x Victory, have been used extensively throughout the world in oat improvement programmes.

Wide experience with S.147 and S.172 during the war years revealed the need for a winter oat intermediate in straw length, but with the yielding capacity of S.147. As a result of a cross between S.147 and S.172, the variety Powys was developed and released in 1957. This variety proved a valuable alternative under conditions where S.147 showed tendencies to lodge, and it soon became the most popular and the most widely grown winter oat.

A significant increase in the yield potential of winter oats was obtained by the release of Penrhyn in 1958 and subsequently Padarn in 1962, both yielding on average over 10% more grain than S.147. Padarn in particular had superior strength of straw and grain quality, and carried a major gene for mildew resistance. It is still retained on the N.I.A.B. Recommended List in addition to the two most recent winter oat varieties released from the Station, namely Peniarth and Pendrwm.

Peniarth is high yielding, resistant to lodging, and carries major genes for resistance to both mildew and stem eelworm. It has become popular in Britain and now appears in the French and Swiss Catalogues of varieties, since it has been found to outyield all the Continental bred varieties by 8-10%. Peniarth has been selected as joint winner of the 1969-70 N.I.A.B. Cereal Award. Pendrwm provides an even higher yield potential, giving over 4% more grain than all other varieties in National Trials, but at maturity tends to lack the straw resilience of Peniarth.

Yield improvements in spring oats have been somewhat less spectacular, but corresponding improvements have been achieved in respect of straw length and stiffness and in the incorporation of disease resistance.

In the early days of spring oat breeding, E.T.Jones placed considerable emphasis on producing varieties adapted to specific environmental conditions, especially upland areas. For extremely poor conditions, S.75 (A.strigosa) and S.171 (A.strigosa x brevis) were selected for their ability to give high yields in the sheaf. For slightly less ex-

treme conditions, the black grained S.79 selected from an old Welsh land race known as Ceirch-du-bach, and S.220 developed from the cross Victory x Radnorshire Sprig, were developed. These gave good yields of straw and grain of reasonable size. The latter has now been replaced by Dyfed, also a black grained variety which has a 12% advantage in grain yield over S.220 in the upland areas.

For soils of moderate fertility a range of varieties was developed, starting with S.175 in 1938. This white-grained variety, developed from a cross of Victory and Black Bell III, tended to produce too much straw on the better soils. It was replaced in 1948 by the high tillering, early maturing Maldwyn (S.221) which was well adapted to a wide range of upland soils, and because of the suitability of both its grain and straw for livestock feeding, it became a popular variety with upland farmers. In 1961 Manod was released; although developed as a general purpose variety, Manod was the first to combine resistance to mildew (Erysiphe graminis), crown rust (Puccinia coronata), and stem eelworm (Ditylenchus dipsaci). Manod is not sufficiently stiff-strawed for the most fertile lowland conditions, but it is specially recommended for the south west of Britain, where crown rust can be a severe problem, and it has also become accepted as a replacement for Maldwyn on soils of moderate fertility.

For the highly fertile soils, where overabundance of straw and lodging are the main problems, early maturing, short-strawed, low tillering varieties were aimed for, and S.84 released in 1938 was more resistant to lodging than any other spring oat variety on the market at that time. However, the most significant improvement in standing ability was achieved with the release of Milford in 1948, which represented the same advance in spring oats as did S.172 in winter oats. Detailed descriptions of all the above varieties and others developed at the Station are given in Leaflet Series S No.8.

The incorporation of resistance to disease, and in particular mildew, has involved hybridization with non-adapted forms often of foreign origin. In the first instance mildew resistance from A. byzantina was incorporated in breeding stocks, but with the emergence of new physiologic races, resistance from other sources has been used. Mostyn released in 1968 is the highest yielding variety of spring oats on the N.I.A.B. Recommended List, is widely adapted, and carries a factor for resistance to the three endemic races of mildew, derived from A. sterilis var. ludoviciana.

Whilst the concept of breeding for particular ecological niches is valid in as far as total yield and ease of harvesting are concerned, in practice there are severe economic limitations to this approach. The most important is that seed of special purpose varieties, especially those specifically developed for the uplands, tends to be very expensive because of the difficulty of producing high yields of seed under fertile lowland conditions without excessive lodging.

Studies of genotype x environment interactions in yield trials over a wide range of environments have shown that, although some varieties are specifically adapted to certain environments, others have a wide range of adaptation and can give high yields over a wide range of environments. As a result of these investigations, greater em-

phasis is now being placed on the development of such varieties with a wider degree of adaptability.

The improvements referred to earlier with regard to winter oats have been effective in nearly doubling the yielding ability of the crop, as observed in the results obtained from a small scale yield trial grown at the Station in 1969. In this trial Grey Winter, a variety typical of the 1920s and early 1930s, yielded 2358 kg/ha compared with an average of 4415 kg/ha from the Station bred Peniarth and Pendrwm. Much of the increase in the national average yields over the last 50 years, as shown in Table 1, may therefore be attributed to the development of improved varieties, the remainder to improved husbandry and fertilizer practice.

Table 1. National average yields (kg/ha) and area sown to three main cereals in England and Wales in 1919 and 1969

Cereal	Million hectares 1919	Million hectares 1969	National average yield 1919	National average yield 1969 estimated	Per cent increase in yield over 50-year period
Wheat	0.899	0.794	1994	4089	105
Barley	0.612	2.066	1744	3675	111
Oats	1.037	0.227	1530	3838	151

It will be noted from Table 1, however, that despite improvements in yielding ability there has been a decline in the area sown to oats as compared with a marked increase in the area under barley.

The increasing importance of barley in western Britain was recognized a number of years ago, and many of the problems now affecting barley were foreseen. With the development of farming systems which combine intensive and often continuous growing of large areas of barley with the practice of growing only relatively few varieties of it, it was inevitable that disease infection should increase. Consequently, the problems of breeding for disease resistance have dominated the barley breeding work during the last 10 years. Most attention has been given to developing short-stiff-strawed segregates resistant to mildew (*Erysiphe graminis* f.sp.*hordei*), leaf blotch (*Rhynchosporium secalis*), the cereal cyst nematode (*Heterodera avenae*), and barley yellow dwarf virus (BYDV). More recently attention has also been given to brown and yellow rust infections which seem to be more intense on material resistant to the other foliar diseases. There are no Station-bred varieties yet on the Recommended List, but a mildew and cereal cyst nematode resistant segregate has been registered with the Plant Varieties Rights Office for a grant of Breeders' Rights.

As far as the other cereals are concerned, breeding investigations have been very limited. Two pure line selections, S.70 and S.72 of the old winter wheat land race Hen Gymro, were isolated in the early years; these gave reasonably reliable yields under very adverse conditions, but were completely unsuited for highly fertile land.

No other varieties of wheat have been released for commercial use. As regards rye, Rheidol was bred specifically for spring forage production and was released in 1965. This variety is very winter-hardy, produces early spring growth and responds to nitrogen application under low temperature conditions.

REVIEW OF RESEARCH ACTIVITIES IN CEREALS

Several important research investigations were carried out in parallel with the breeding programmes during the period under review. Most of the early genetical research studies in oats were concerned with the genetic mechanism controlling the appearance of fatuoids in cultivated varieties (16). Other studies extended to cover the diploid and tetraploid Avena species as well as the hexaploids, were designed to gain further knowledge of genome relationships in Avena (5). These have subsequently led to the current intensive programme, carried out in co-operation with the Cytology Department, into the transfer of valuable genetic factors, and in particular genes for disease resistance, from diploids and tetraploids into the hexaploid oats. The discovery of a new species A. magna and living specimens of A. ventricosa (21) on the joint W.P.B.S./Canada Department of Agriculture expedition to the Mediterranean region in 1964, added impetus to this programme.

Most of the early work on disease was concerned with seedling blights and their chemical control. In the absence of known factors for resistance to other diseases, except crown rust for which Red Rustproof provided effective resistance, the breeder had to concentrate on selecting in the field for low levels of disease in the crop. The success of this action is reflected in the performance of the Station varieties, most of which suffer less from endemic disease attack than other more exotic varieties.

The resistance of Red Rustproof to crown rust was effective against only a few races and soon succumbed to attack. However, a later search revealed resistance factors in Bond, Tama and Victoria which remained effective until 1952-3, when two new races of the rust capable of attacking these oat varieties were identified at the Station. Following further glasshouse studies and genetic investigations (4), Landhafer and Santa Fe were introduced into the breeding programme. A measure of the importance of crown rust resistance may be obtained from the results of two N.A.A.S. trials in Pembrokeshire during the severe crown rust epidemic in 1961. The yield of Manod, which has resistance from Tama, was unaffected by rust infection, whereas the susceptible variety Condor suffered a 27% reduction in grain yield.

Powdery mildew (Erysiphe graminis) has always been recognized as a major foliar disease of cereals in the western part of Britain. Continuous selection for relative freedom from this disease in the breeding nursery has led to the useful level of adult plant resistance expressed in Maldwyn and Maelor which is exhibited irrespective of changes in the virulence genes of the pathogen. Intensive screening of the Station oat collection in the late 1940s revealed a factor for resistance in Red Algerian and some selections derived from it. One of these was used in the development of Manod, Padarn, Peniarth and Pendrwm. It is possible that the greatly increased yield poten-

tial of these latter three varieties can be largely attributed to this introduction of exotic germ plasm into the breeding programme. Further major genes for resistance in hexaploid, tetraploid and diploid oats have since been isolated, but because of the facility with which the fungus produces new races, such factors tend to be overcome soon after the resistant varieties are grown on a large scale. Their use has demonstrated, however, that powdery mildew can cause up to 39% reduction in grain yield following a severe epidemic (19).

The soil-borne diseases pose a real threat to cereal production even in the west of Britain where cereals, though not comprising a large proportion of arable land, tend to be grown frequently on the same fields, often the only ones suitable for arable cultivation on the farm. Special attention has been given to nematode resistance, first to the stem eelworm (Ditylenchus dipsaci) of oats and later to cereal cyst nematode (Heterodera avenae) in oats and barley. The former can cause complete crop failure, but in investigations commenced in 1950 it was found that a single dominant gene for resistance was present in some of the earlier Station varieties (3). This resistance incorporated in high yielding varieties such as Peniarth, has remained fully effective against all populations of D. dipsaci. However, H. avenae presents a greater threat since it is more widespread and can attack oats, barley, wheat and certain grasses. Results of extensive investigations have shown the existence of distinct races of the nematode affecting different barley genotypes. Extensive genetic investigations by Hayes and Cotten (11) have shown that there are at least four genes controlling resistance to H. avenae in barley, the most effective of which has already been used in a breeding programme to produce a nematode resistant variety.

The above review indicates the emphasis that has been placed on research into diseases and pests which has resulted in real benefits in terms of development of resistant types. Other aspects have also been pursued but with less positive success. Frit fly is a widespread pest of spring oats, but detailed examination of various reputedly resistant genotypes has shown that the genetic differences between varieties are small and expressed either in respect of insect preference, which is not likely to operate in the absence of choice of varieties for egg laying, or through rapid seedling development acting as an escape mechanism.

The earliest agronomic investigations established the need for better cultural practices and reliable seed to achieve the best yields of oats. More recent agronomic studies showed that, with proper management, oats could provide useful spring grazing without detriment to the grain crop (8). Detailed studies on the effects of seed rate on the morphological and yield characteristics of varieties of spring oats gave an insight into the interrelationship of the various components of yield and indicated which components could most likely be altered by breeding to achieve improved yield (17, 18).

The past 50 years have seen major changes in the technology of breeding, particularly in the development of biometrical statistical techniques applicable to the study of continuous variation. In recent years research had been concentrated on the de-

velopment of techniques for the choice of appropriate parents in breeding programmes, using information resulting from the analysis of data from the early generations of diallel crosses for the improvement of quantitatively inherited characters (9). Investigations into the complexities of genotype-environment interactions have also been carried out, and on a more fundamental basis, experiments have been conducted in co-operation with research workers in the U.C.W., Department of Agricultural Botany. to assay the contribution of individual chromosome segments to varietal performance.

An important discovery at the Station was the finding of the genetical basis of reaction to the phytocidal action of DDT in barley and location of the recessive gene for resistance on chromosome 7. This discovery has led to schemes for the production of hybrid barley employing linkage of the ddt gene with a recessive gene for male sterility. In addition, the discovery of the DDT reaction and variation in response to barban gave impetus to the concept of breeding for reaction to chemicals to increase either resistance to herbicides, thus giving a greater margin of crop safety, or the ability to absorb and translocate systemic insecticides or fungicides most efficiently.

CURRENT BREEDING AND RESEARCH PROGRAMME

Winter oats

1. Breeding

The main objectives in the winter oat breeding programme are the development of winter-hardy, high yielding varieties with good grain quality and resistance to lodging, mildew, crown rust, cereal cyst nematode and soil-borne virus infection.

The most advanced breeding material consists of segregates from crosses designed to combine moderate length of straw with high yield of grain of good quality and resistance to mildew races 2, 3 and 4 originating from Cc 4146 and A. sterilis var. ludoviciana (Cc 4346).

From amongst populations segregating for crown rust, eight resistant families containing the major gene for resistance from Ascencao have been isolated for yield trials.

Lines providing high yields of dry matter for early spring grazing have been selected for several generations. The results of a yield trial conducted in 1968/9 indicated that one line, 02801 Cn/47, produced significantly more dry matter in early spring than Pendrwm.

This segregate is being reselected to isolate a uniform stable line for final trials and possible consideration for registration as a new variety.

2. Controlled freezing tests for winter hardiness

One of the major problems in the improvement of winter oats for Britain is the lack

of adequate winter-hardiness in existing varieties which renders them liable to severe damage in colder-than-average winters. To facilitate breeding and research, artificial freezing tests using controlled environment facilities have been developed by T. D. Johnston.

A seedling damage test (25) using these facilities has given results corresponding closely to observations in the field over a number of years. The amount of seedling damage is assessed in the glasshouse after a standard period of freezing following hardening for 7 days at +2° to +5°C under 8 hr photoperiod. Assessment of a range of exotic genotypes has indicated a few which exhibit greater hardiness than that present in British varieties. The maximal level so far found, however, is not comparable to that existing in the other winter cereals and a search for transgressive segregation for this character amongst the progenies from crosses between the existing hardiest types has been commenced. The assessment technique is also being used as a direct selection tool in the breeding programme; following tests on segregating populations, the least damaged survivors are grown on. Unfortunately, however, because the most hardy lines generally have poor grain quality, weak straw, and high susceptibility to disease, further hybridization and selection will be necessary before the material can be considered eligible for yield trials.

Further critical investigations of the experimental technique were carried out to assess the importance of various environmental factors during initial seedling growth and hardening (C.Y.Cho, unpublished). A range of varieties of wheat, barley, rye and winter and spring oats was used in the investigation. The main conclusions drawn from the results were as follows:

(i) High temperatures (20°C) during the germinating and pre-hardening period prevented the development of potential hardiness of varieties classified as intermediate. Those classified as very hardy or non-hardy were unaffected. The addition of fertilizers to the growing medium of compost at sowing time produced variable effects and requires further investigation.

(ii) The development of hardiness occurred more rapidly at +5°C than at +2°C, but variation in photoperiod from 8 to 16 hr had little or no effect. Under the favourable temperature, a hardening period of 4 days was sufficient for the development of characteristic varietal differences. Exposure for 24 hr to a temperature of 15°C after 7 days hardening resulted in significant loss of hardiness. At higher temperatures the loss was even more rapid.

During both the pre-hardening and hardening period the restriction of water supply resulted in greater expression of hardiness, but in practice application of water stress is not recommended because of the difficulty in obtaining uniform conditions.

Estimates of water soluble carbohydrate (WSC) were made on samples of vacuum dried material from a number of treatments. Within any variety the changes in hardiness generally corresponded positively with changes in WSC content. The mean species differences in WSC, however, did not correspond with the hardiness ranking of the species.

3. Soil-borne oat mosaic virus

The winter oat yield testing programme at the Station in 1968/69 received a setback because a high proportion of the small scale yield trial plots was severely infected with soil-borne oat mosaic virus (SBOMV). However, it was possible to identify the most susceptible genotypes by comparing their performance at the non-infected centres at Seale Hayne, Devon, and Morley, Norfolk, with that obtained in the Station trials. In particular, segregates having either Powys, Padarn or Pendrwm as parents yielded nearly twice as much grain at the infested site as segregates from other crosses.

An area of land heavily infested with SBOMV has now been set aside for breeding and research investigations on this virus in collaboration with the Plant Pathology Department. From experiments on this land in 1968/9 it is clear that selection for high tolerance to the virus can be conducted in the field, since several selections with apparently high levels of tolerance were consistently identified. In order to determine the relationship between this virus and SBOMV as described by other workers, 22 lines from G.M.Wright, D.S.I.R., Christchurch, New Zealand, and other lines from various workers in the United States were included in a replicated trial. However, since most of the material was not sufficiently hardy to survive the winter, glasshouse screening tests are now being devised to continue this study and also to include resistance to SBOMV in the breeding programme.

Spring oats

1. Breeding

In view of its wide adaptability, the variety Mostyn resistant to races 1, 2 and 3 of mildew is now being used extensively by D.A.Lawes in breeding programmes which will also incorporate resistance to crown rust, cereal cyst nematode and manganese deficiency. In spite of the superiority of the yielding ability of oats, compared in national trials with other spring cereals, farmers are still reluctant to devote a large proportion of their arable land to this crop mainly because of the hazards which accompany a delay in harvesting, and problems of intensive utilization especially by non-ruminants. Although the straw of the more recent varieties of both spring and winter oats is shorter and stiffer, and the grains are more securely held in the panicle, it has not been possible as yet to combine the more extreme forms of shortness and stiffness with high yield, as has been accomplished in the dwarf and semi dwarf types of wheat and barley.

Although Milford and S.172 have short, strong straw they also have compact panicles and are not as high yielding as other varieties under moderate levels of fertility. Unfortunately, neither Milford nor S.172 have proved to be good parents, as it has not been possible to isolate high yielding short-strawed segregates with less compact panicles from progeny following hybridization with other high yielding parents. The genetic system governing straw length in a range of spring oat parents (including Milford) has been studied in a diallel crossing programme. Following selection in the F_2 and

F_3 generation, F_4 populations are now being subjected to yield trials in order to assess the strength of the correlations between plant height and grain yield.

The positive correlation between length of straw and grain yield in the Milford crosses remains unbroken. This is illustrated by the results presented in Table 2, which gives the average plant heights and grain yields of F_4 populations of two crosses(Condor x Milford and Condor x Pendek) bulked according to height groups in the previous generation.

Table 2. Plant height and yield of selected F_4 populations from two crosses of spring oats. (Data expressed as per cent of the mid-parent value of the two parents involved)

Cross	Height group, F_3 generation (cm)	Plant height (cm)	Grain yield (g/plant)
05722 Cn.			
Condor x Milford	81-90	96.7	95.3
	91-100	102.6	101.9
	101-110	107.2	105.7
	111-120	108.2	106.3
	121-130	109.8	97.8†
05720 Cn.			
Condor x Pendek	101-110	98.2	86.8
	111-120	105.1	89.9
	121-130	104.5	88.1
	131-140	110.3	77.2

† yield reduced due to lodging

The mean heights and ranges of the two F_4 populations are similar, but in the cross involving Milford, plant height maintains a close correlation with grain yield. On the other hand, this relationship does not appear to hold for the Condor x Pendek population. Further yield tests on land under different levels of fertility will be necessary before the full relationship between yield, height and lodging resistance can be established.

Meanwhile further attempts are being made to produce new short-strawed genotypes by the use of ethyl methane sulphonate to induce mutations. Plant height can be easily recognized and precisely measured in large populations and should, therefore, be a suitable character for handling by this technique.

In addition to improving straw strength we are attempting to develop techniques which will enable breeders to produce types with an even higher yield potential.

Earlier endeavours to improve yield and to analyse environmental interactions by studying morphologically expressed components of yield have proved disappointing. An increase in any one morphological component is commonly balanced by a compensatory decrease in some other component. The prime consideration, therefore, must be to increase the total dry matter accumulation. In an effort to accomplish this, physiological components of yield, and in particular photosynthetic activity, are now being studied in detail.

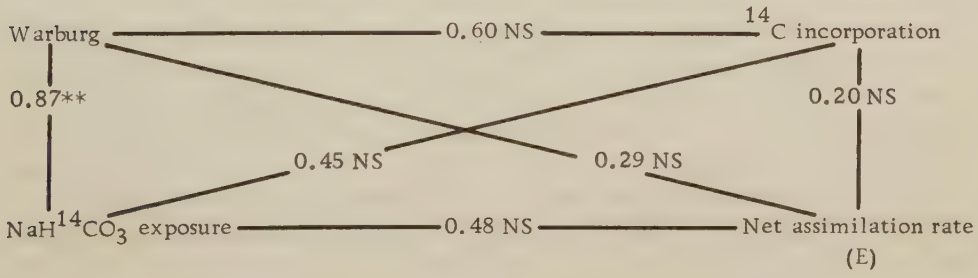
2. Physiological aspects of yield and phenotypic stability

The basis of all crop yields is the utilization of light energy to produce dry matter, and provided water and soil nutrients are not limiting, the ultimate yield is determined by the factors which influence this process and the way they are integrated both within the plant and within the crop. The production of dry matter by a crop is a function of the area of the chlorophyll containing parts of the plants and the related photosynthetic activity. An analysis of the influence of each of these attributes on yield must be complex, but in the first instance at least, these attributes can be analysed into more simple physiological components which can be examined individually. Photosynthetic activity per unit leaf area is one of these criteria.

Varietal differences in photosynthetic activity of cereal leaves are being investigated by D.A.Lawes in collaboration with K.J.Treharne, Developmental Genetics, using the following techniques: (a) Warburg manometric, (b) ^{14}C incorporation from $^{14}CO_2$, (c) ^{14}C incorporation following $NaH^{14}CO_3$ exposure, and (d) estimates of net assimilation rate (E) derived from growth analysis.

The degree of agreement which has been found between these four techniques is illustrated in Fig.1 which presents the correlation coefficients between results obtained from seedling leaves of ten varieties of oats.

Fig.1. Correlation coefficients for results of photosynthetic activity as measured by four different techniques



The results obtained by the Warburg manometric technique and $NaH^{14}CO_3$ exposure are the most comparable as both these techniques measure photosynthetic activity in cut sections of detached leaves over short periods of time. On the other hand, estimates of activity by either ^{14}C incorporation from $^{14}CO_2$ and the derived values of E were from whole plants, and therefore these results will have been influenced by trans-

location patterns.

When the advantages and disadvantages of the different techniques are considered, and these include the higher running costs and the additional formalities of handling labeled carbon, it is evident that the Warburg manometric, which provides good comparative estimates with a reasonable degree of reproducibility, is the most suitable technique for screening material in a breeding programme.

An example of the genotypic differences which have been found is presented in the following extract of data of measurements of flag leaf photosynthesis of five varieties of oats.

Variety	Warburg (microlitres $O_2/cm^2/min$)
Maldwyn	1.70
Condor	1.69
Victory	1.43
Castleton Potato	1.29
Yielder	1.20
S.E.	$\pm$0.035

The differences of 40% suggest that photosynthetic activity of flag leaves may be of value as a criterion in a plant breeding programme, and the Warburg manometric technique is being used to screen populations for this character. It will also be used to examine photosynthetic activity of parts of the inflorescence.

3. Disease investigations

Mildew (Eryisphe graminis f.sp. avenae) isolates collected by collaborators in the National Physiologic Race Survey have been multiplied and identified by I.T.Jones. Race 2 which is avirulent on Mostyn continues to be the most prevalent in the country. However, further isolates were obtained from the breeding nursery in 1969, which are virulent on Mostyn and give race 4 and 5 type reactions. Cc 4146 resistant to race 4 was slightly infected towards the end of the growing season, and isolates from these plants proved to be of the race 5 type, which is virulent on both Mostyn and Cc 4146. Although race 5 has been detected previously in the glasshouse, this is the first record of its occurrence in the field. So far, no source of resistance effective against this race has been found in hexaploid oats, but the resistance of the wild diploid Cc 3678 (A.strigosa ssp.hirtula) and the tetraploid Cc 4897 remains effective against all isolates.

In collaboration with Hugh Thomas of the Cytology Department, work has continued on transferring the mildew resistance of Cc 3678 into hexaploid oats. Large populations derived from 43-chromosome lines were self-pollinated and the progeny screened for mildew resistant 42-chromosome recombinants which would have the hirtula gene

substituted into the hexaploid chromosome complement. Such recombinants have not yet been detected, because the expression of resistance is low when the hirtula gene is present as a single dose in a hexaploid background.

A much higher level of expression in a hexaploid background is obtained when the tetraploid Cc 4897 is used as a donor parent and a parallel programme to substitute this gene for resistance into hexaploid types is being carried out. Another diploid, A. ventricosa Cc 4852, has been found to be resistant to races 2, 3, 4 and 5, and is being intercrossed with a view to transferring its resistance factor(s) into commercial hexaploids.

The presence of isolates virulent on all available hexaploid sources of resistance at the seedling stage, and the rapidity with which major gene resistances have been nullified since 1960, have resulted in renewed interest in non-specific resistance. This type of resistance, designated adult plant resistance (APR), is effective against all known races and can be expected to be more permanent than immune or hypersensitive reactions conferred by single genetic factors.

Differences in level of infection between genotypes may be due to several characters. Using the detached leaf method, segments from leaves of oat plants at the 5th leaf stage were inoculated with a moderate concentration of spores. The following results (Table 3) typify the characteristics recorded on genotypes differing in levels of adult plant resistance.

Table 3. Differences in infection characteristics of three oat genotypes inoculated at the 5th leaf stage (mean of 5 leaves)

		14 days after inoculation	
Degree of non-specific resistance	Days to first appearance of mildew	% leaf segment area infected	Vigour of pustules (0 = no sporulation 10 = profuse sporulation)
Very low	4.2	84	9.5
Moderate	6.0	46	9.2
Very high	6.4	6	3.0
S.E.	±0.4	±4.1	±0.4

The genotype with a moderate degree of resistance compared with that having a very low resistance, showed a delay of two days in the appearance of mildew symptoms and a marked reduction in area infected, although there was no difference in the vigour of the fewer pustules which developed. The genotype with a very high level of resistance showed a further significant reduction in area infected and in the vigour of pustules.

The combined effect of the three characteristics markedly influences the number

of spores released for reinfection. An estimate of the number of spores produced by these genotypes over a 15-day period revealed an 80-fold difference between the two extreme types of resistance. The growing of cultivars which have a low rate of spore production, although not immune, would thus undoubtedly reduce the level of inoculum and hence the level of field infection.

The genetic control of APR is being studied in F_2, F_3 and subsequent generations; results obtained so far indicate that the inheritance of these factors is complex.

The crown rust (Puccinia coronata f.sp. avenae) resistance breeding programme has been based on the resistance genes from Landhafer, Santa Fe and Ascencao. These genes have consistently shown high resistance to British crown rust races. However, a pathotype virulent on Landhafer and Santa Fe was detected by B.C.Clifford in the 1969 National Physiological Race Survey. Fortunately, Ascencao is immune to this race. Advanced winter and spring segregates were tested in the field under heavy induced epiphytotics of race 229 in 1968 and race 232 in 1969. This enabled positive selection to be carried out for material carrying resistance from Ascencao which contains the gene from Victoria and gene E. In addition a backcross programme is being carried out to introduce Ascencao resistance into Mostyn.

Among the hexaploid oats, Cc 4658 Avena sterilis (C.I. 376), certain Avena byzantina genotypes, notably Cc 4698 (C.I. 2863), Cc 4699 (C.I. 3445), Cc 4700 (C.I. 5194) and Cc 4701 (C.I. 175021), and the Australian cultivar Cc 4826 (Mortgage Lifter), seem to be most promising as sources of resistance to cereal cyst nematode (Heterodera avenae). Cc 4658 has been tested against a range of populations of the nematode with different expressions of pathogenicity to spring barley, and only limited cyst development has been found on this genotype against all populations. Accordingly, this resistance factor is now being incorporated into adapted genotypes of both spring and winter oats. The cereal cyst nematode resistance breeding programme has reached an advanced stage. Homozygous cyst nematode resistant lines with a Peniarth background are included in yield trials and are also being reselected to produce stable lines. In addition, comparable homozygous resistant and susceptible lines are being increased in order to provide seed for trials to assess the effect of the nematode on oat yields (Plate 1).

Barley

1. Spring barley breeding

The best segregates from the early barley breeding programmes are now reaching a stage of homozygosity where they can be finally evaluated as potential varieties. The first segregate to be selected for further multiplication is 7187 Co 4/31/69; it has been named Sabarlis and was submitted to the Plant Varieties Rights Office (PVRO) for inclusion in Index Trials in 1968 and Statutory Performance Trials in 1969. The development of this variety provides a good illustration of the amount of selection, testing and multiplication work which is involved in producing a new cereal variety

Plate 1. Cereal cyst nematode Heterodera avenae

(a) Contorted root system of susceptible oat cultivar grown on infested soil.

(b) Portion of root system showing mature females attached to roots.

and is diagrammatically represented in Figure 2.

A genotype (Cb 824) obtained from Professor S. Andersen, R.V.C., Copenhagen, known to be resistant to pathotypes 1 and 2 of the cereal cyst nematode, was crossed with Rika (Cb 545) in 1960 and the F_1 backcrossed to Cb 788, an adapted segregate having the Mla_6 gene for mildew resistance derived from H. spontaneum. The eelworm-resistant backcross progenies were grown and their progenies tested for mildew resistance and assessed for agronomic performance. Selections from these were progeny-tested for mildew resistance in the glasshouse and only homozygous resistant genotypes were retained.

Further cycles of selection for agronomic performance, and parallel tests for eelworm and mildew resistance were carried out in the glasshouse and field between 1964 and 1967, with between 1150 and 3440 progeny rows being critically assessed in each year. In 1967 sufficient seed was available for selected lines homozygous for mildew and nematode resistance to be included in yield trials. At the same time it was also possible to obtain detailed assessments of straw strength, uniformity of ear emergence, DDT reaction and other characters. Ten drills, all representing one F_5 backcross family, were selected from amongst the 2110 ear row progenies sown in 1967 to form the basis of the new variety.

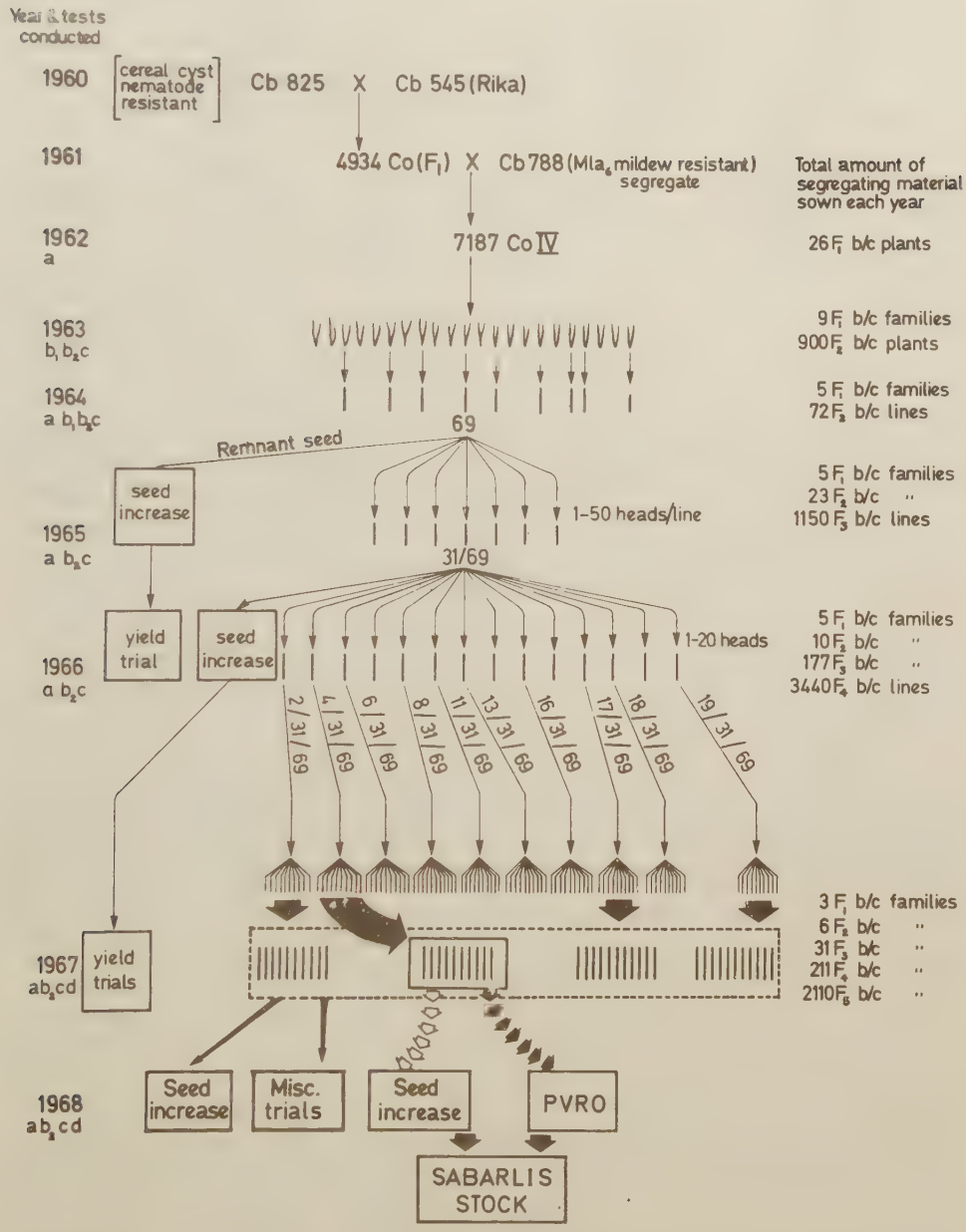
From this stage onwards parallel lots of ears and seed bulks have been used for PVRO trials, further Station yield trials and large scale multiplication.

Thus, it will have taken nearly 10 years of testing, selection, reselection and multiplication to produce an adapted variety which combines the Ha gene conferring resistance to pathotypes 1 and 2 of Heterodera avenae, with the gene Mla_6 for mildew resistance. Its yield has not been significantly different from that of Zephyr and Rika when tested on cyst nematode-free land of moderate fertility but. as indicated by the results given in Table 12, Sabarlis can be expected to outyield similar susceptible varieties by up to 8% on cyst nematode infested land. Its straw stiffness is not as good as that of some recently introduced varieties on land of high fertility, consequently current breeding programmes are concentrated on developing nematode resistant segregates with higher yield potential, stiffer straw and other major genes for mildew resistance. In addition, programmes are being pursued to combine in high yielding genotypes the Ha gene with a recessive gene for resistance to the currently relatively rare pathotype 3 of H. avenae.

In the less advanced breeding material, lines have been selected for extreme shortness and stiffness of straw and good agronomic quality. Thirty of the most promising F_6 and F_7 lines homozygous for Mla_6 were grown in two balanced lattice trials at four centres in 1969.

The range of height and yield values compared with Abed Deba is shown in Table 4.

Fig. 2. The development of Sabarlis



Key to tests: a = cereal cyst nematode; b = mildew (1 glasshouse; 2 = field); c = agronomic performance; d = replicated yield trials

Table 4. Height and yield of short stiff-strawed spring barley segregates at four centres in 1969

Trial centres	Height (cm) Abed Deba	Height (cm) Segregate range	S.E. ±	Range of yield of segregates Abed Deba = 100	S.E. ±
Gogerddan 60 units N	65	51-61	2.09	87-105	3.35
Gogerddan 120 units N	75	58-73	1.91	89-104	2.96
Seale Hayne, Devon	63	47-58	2.20	94-112	2.36
Hedley Hall, Tadcaster	65	49-62	1.40	97-122	3.05
Morley, Norfolk	-	-	-	99-124	4.36

Although there was 22% overall increase in grain yield as the result of applying additional 60 units of N at Gogerddan, there was no significant nitrogen level x genotype interaction. Whilst these lines combine resistance to specific races of mildew; high yield, and extreme shortness of straw, under certain conditions they appear to be prone to straw shattering. Although this characteristic has not been observed in yield trials, it has been a feature of material in progeny rows which have been left in the field until after the combine ripe stage. Results obtained from supplementary experiments, in which these short-strawed segregates have been sprayed with Zineb and Mancozeb at 10-day intervals, indicate that some pathogen or nutrient unbalance may be responsible for this straw shattering. It is clear from the results so far that research work will be needed before the benefit of these short-strawed segregates can be fully exploited by the breeder.

Special programmes to produce uniculm and huskless genotypes are proceeding satisfactorily, although many of the advanced huskless segregates exhibited a high degree of sprouting during the 1969 harvest. One of the huskless segregates has proved valuable for GA_3 bioassay work, as it is more sensitive than any other variety previously tested. Progress with breeding programmes designed to introduce major gene and adult plant non-race-specific resistance to mildew, brown rust, yellow rust, and leaf blotch into adapted genotypes is discussed in detail in later sections.

2. F_1 hybrid barley investigations

During recent years some research work has been carried out to obtain more information on the extent and range of variation in seed setting of male sterile plants following wind pollination, and on the extent of heterosis and its expression under different conditions of competition. In addition, further genetic information needed to operate the Balanced Tertiary Trisomics (BTT) method of hybrid seed production has been obtained. Furthermore, adapted female lines are being developed in order to produce large quantities of F_1 hybrid seed for further investigational work and, if needed, for use in commercial hybrid seed production.

A summary of the results obtained after wind pollination of male sterile genotypes

from four reasonably well adapted varieties with two of the more promising pollen donors is given in Table 5.

Table 5. Per cent seed set on male sterile segregates from four varieties in 1968 and 1969 (6 replicates)

♀ Male sterile receptor parent	Pollen donor: Impala 1968	Impala 1969	Maris Concord 1968	Maris Concord 1969
Freja (Cb 1000)	19.8	28.7	30.9	19.6
Herta (Cb 1002)	10.1	6.7	16.3	11.2
Carlsberg II (Cb 1003)	15.1	6.2	21.0	9.5
Sv.50/109 (Cb 1005)	33.6	15.8	33.2	28.9

The results confirm previous experience that Freja and Sv.50/109 produce more seed when used as female parents than Herta or Carlsberg II. The maximum seed set registered in the past four years has been remarkably constant, around 34%. The seed set obtained on male sterile diploid plants from the 63-j-18-17 BTT stock kindly provided by Dr. R. T. Ramage of Tucson, Arizona, placed amongst plots of various pollen donors flowering at the same time, varied from 6.2%-23.6%.

A series of replicated yield trials of F_1 hybrids and their pollen parents was grown at the Station during 1969. It included material kindly supplied by Dr. Ramage, and the Northrup King Seed Co., of Minneapolis, as well as F_1 hybrids produced at the Station. Certain F_1 hybrids yielded significantly more grain than their pollen parents, but since the female parents of F_1 hybrids produced by the BTT technique were not available for comparison, it is not possible to determine whether the F_1 hybrids were significantly better than the best parent. As expected, the material from the United States was not adapted to British conditions but, when grown under low levels of fertility, harvestable crops were obtained.

Of particular interest were the results of a replicated drilled plot yield trial in which the F_1 hybrid Hembar was compared with its pollen parent Arivat. In this trial it yielded 25% more grain than Arivat, although even with this superiority it gave less than 70% of the yield of the controls Impala and Zephyr.

The F_1 hybrid grain obtained from the experiments on wind pollination (see Table 6) was included in trials sown at a spacing of 150 x 50 mm and 300 x 300 mm in 1968 and at four different spacing in 1969. In both trials the plants grew well but in 1968 there were symptoms of a fairly severe infection of barley yellow dwarf virus (BYDV) just after ear emergence. In the 1968 trials the per cent differences between the F_1 and the mid-parent value for each individual F_1 varied from +0.94 to +7.19 at the wide spacing and +0.91 to +2.66 at the close spacing.

In 1969 only F_1 hybrids from the crosses Freja x Impala, Sv.50/109 x Impala, Freja

x Maris Concord, Herta x Maris Concord and Sv.50/109 x Maris Concord were included in the yield trials, but there were more spacing treatments and increased replication. A summary of the mean performance of the F_1 hybrids compared with their weighted mid-parent values is given in Table 6.

Table 6. Comparative performance of five European F_1 hybrids (F_1) and their mid-parent (MP) values. Aberystwyth 1969

Mean values per plant	Spacing treatment							
	25 x 25 mm		50 x 50mm		100 x 100 mm		200 x 200mm	
	F_1	MP	F_1	MP	F_1	MP	F_1	MP
Wt of grain (g)	0.79	0.64	1.75	1.25	4.63	3.45	11.2	8.43
Wt of straw (g)	0.95	0.93	1.99	1.57	5.69	4.56	13.9	12.2
No. of primary tillers	1.00	1.00	1.69	1.29	4.01	3.31	8.24	5.66
No. of secondary tillers	0.56	0.52	1.04	0.77	1.78	1.46	4.97	4.70
1,000 grain wt (g) (P)†	39.4	37.7	41.9	40.9	45.6	43.1	47.7	46.8
1,000 grain wt (g) (S)†	27.2	27.1	29.9	28.6	30.4	30.0	30.1	28.6

† P = Primary tillers; S = Secondary tillers

The mean yield of grain produced per F_1 plant was significantly greater than that for the parents at all spacings, and there is no evidence of any interaction between F_1 hybrids or parents at the different spacings.

The mean increases of 24%, 40%, 34% and 32% at each of the decreasing densities are far greater than those measured in any of our previous trials with this material (10). There is no obvious reason for the increased magnitude of this heterotic effect which was consistent over all five crosses in this season. In each case, not only were the values for the grain yield of the F_1 hybrids superior to their mid-parent value, but they were also better than those for the best parents. As can be seen from Table 6, the heterosis for grain yield per plant represents a cumulative effect of superiority in each of the components measured at every spacing.

The $\underline{ms}_2$ gene located on chromosome 2, and the translocation break-point T_2 - 7$\underline{d}$ together with a gene located on chromosome 7 controlling seedling lethality are being backcrossed into four recurrent parent lines, viz. Zephyr, Impala, Isaria and a short-strawed Station segregate, in a scheme to produce adapted BTTs which will yield male sterile diploids without resort to hand roguing. However, it is not yet clear whether the linkage of ms_2 and the breakpoint of T_2 - 7$\underline{d}$ and the seedling lethal gene is sufficiently close for the system to operate successfully on a large scale.

Ergot was found to be quite common on the various male sterile parents grown in the nursery. This fungus is often found on grasses in the locality of the Station, but seldom on cereals. It is possible that, with increased selection towards characters which increase seed setting following wind pollination, ergot will increase in frequency

and pose a real problem in producing F_1 hybrids on a field scale, unless a systemic fungicide can be found to control the pathogen.

3. Disease investigations

(1) Mildew (Erysiphe graminis f.sp. hordei)

Two lines of approach are being followed in an attempt to reduce yield losses due to barley mildew. First, in spite of the rapid rate with which new physiologic races of the pathogen emerge, major genes for race specific resistance are still being incorporated in adapted high yielding genotypes, but wherever possible into a background of non-specific resistance. In order to do this effectively, major genes for resistance have to be identified and their genetic interrelationships with respect to differing physiologic races determined. The rapid rate of appearance of new virulence genes in the pathogen is well illustrated by two new physiologic races recently identified at the Station by I.T.Jones. The first was isolated in the glasshouse during the autumn of 1968; it produced a susceptible type 4 reaction on the hitherto resistant Emir and Sultan and, except for its reaction on the latter two varieties, was identical with C5 when tested on the German set of differentials. This new race has been designated AB3 to distinguish it from the C5 type culture avirulent on Emir (AB2). The other race was found in the field in 1969. It produced a type 4 reaction on Emir and Sultan. This is the first time it had been observed in the nursery. This isolate differed from AB3 since it was avirulent on genotypes having the Mla_6 gene. Such new races provide useful tools to study the genetics of host/pathogen relationships. AB3, A0, and C7 type races are being used to determine the interrelationships of the genes controlling race specific resistance from reactions of the F_1, F_2 and F_3 generations of a 12-parent diallel which includes most of the German mildew differential varieties together with Emir, Monte Cristo, M.C.20 and Grandpa. In the breeding programme all the segregates having genes from Mianwali, Engledow India and Monte Cristo have maintained their resistance to all the new isolates.

In the second approach, techniques similar to those used for oats are being used to screen barley genotypes for non specific or adult plant resistance. Over 70 genotypes have been grown in spore-proof conditions, and leaf segments were sampled and tested at successive growth stages to ascertain levels of resistance. The same genotypes have also been sown at two dates in the field, and mildew recorded at different stages of development. Mildew infection scores are given in Table 7 for five of the genotypes which have shown susceptible reactions as seedlings (against three races including A0), but varying levels of resistance at the adult plant stage. The genotypes Minerva, Vada and Abyssinian 16 show a high level of resistance, Archer is intermediate, while Bigo is fully susceptible at both seedling and adult plant stages of growth.

There is fairly good agreement in these genotypes between detached leaf and intact plant reactions at both growth stages and with field assessments. However, of particular interest from a screening and selection point of view is the fact that Minerva, Vada and Abyssinian 16 had a lower degree of infection than the other genotypes, even

Table 7. Mildew resistance in five selected barley genotypes

	Glasshouse†				Field*	
	Detached leaves		Intact leaves			
	Seedling	Adult	Seedling	Adult	Seedling	Adult plant
1. Minerva	50^3	0^0	60^3	0^0	4.0	1.0
2. Vada	80^3	15^3	50^3	5^1	4.5	1.5
3. Abyssinian 16	45^3	4^1	60^3	10^1	4.0	1.0
4. Archer	80^4	8^3	100^4	30^2	5.0	2.0
5. Bigo	100^4	80^4	80^4	90^4	5.0	4.5
Growth stage at time of scoring	2-leaf	At heading	2-leaf	At heading	Mean of 1st four leaves	At heading

Disease score † % of leaf segment or leaf area infected; superscript = reaction type (0-4) scale 0 = immune, 4 = very susceptible
* A general score (0-5) 0 = completely immune, 5 = very susceptible

at the seedling stage, when tested as intact seedling or detached leaf, and they also gave the highest level of resistance as intact adult plants in both glasshouse and field tests.

(ii) Leaf blotch (*Rhynchosporium secalis*)

With the increased intensity of barley growing in the western half of the country some diseases which were formerly of minor importance began to cause concern. The most evident of these is leaf blotch, which by 1962 had reached a devastating intensity in Cornwall and Devon, and the barley breeding programme was thus expanded to include resistance to this disease as one of its main objectives. The first Station programme utilized resistance derived from the varieties Atlas 46, Turk and Osiris, but concurrent research investigations showed that Atlas 46 and Turk contained the same resistance genes, and the segregates containing genes from the very poorly adapted Turk parent were discontinued. The Osiris crosses were also poorly adapted, and were continued at low priority. Full attention was given to the Atlas 46 resistance source, which had been exploited in crosses with Station selections and later in backcrosses to Zephyr, Impala, Deba Abed, Sultan and Emir.

This programme received a setback when it became apparent that a race of *R. secalis* capable of attacking Atlas 46 existed in Britain. Moreover, *R. secalis* infection had continued to extend to other areas in the country. The breeding programme was further expanded in 1966, to seek new resistance sources and to carry out more detailed investigations of all aspects of *R. secalis*, including both race-specific and non-race-specific resistance to the disease.

Investigations on the inheritance of resistance in 16 barley introductions of diverse origins and agronomic characteristics have now been completed by R. M. Habgood. For these tests, the pathogen population was represented by cultures of three biotype groups obtained from Dr. H. Owen, University of Reading, the biotype groups being A (U.K.-2) and B (U.K.-1), and C, respectively. The latter is distinguished from its nominal 'B' classification by pathogenicity on the supplementary differential Modoc. The results showed that in these 16 varieties there are seven resistance gene systems which are effective against the known British biotypes of R. secalis (see Table 8), but only two of the systems, (iv) and (v), are effective against all the biotypes.

Table 8. The reactions of seven identified resistance gene systems to the three British biotypes of R. secalis

Resistance gene system		Varieties	Reaction to biotype groups A	B	C
(i)	Dominant	Atlas 46, Turk, Brier, Hudson, Dea	S	R	R
(ii)	Dominant	Modoc	S	R	S
(iii)	Incompletely dominant	Wisconsin Winter x Glabron	S	R	R
(iv)	Two complementary dominant	Osiris, La Mesita, Gembloux 14, C.I.3515, C.I.8256	R	R	R
(v)	Two complementary recessive	Jet	R	R	R
(vi)	Recessive	Nigrimudum	S	R	R
(vii)	Recessive	C.I.4364, C.I.4368	S	R	R

(S = susceptible; R = resistant)

The breeding programme associated with these investigations is now designed to combine resistance from Jet and C.I.8256 with adapted germplasm from Maris Badger, Zephyr, Impala, Julia and Vada. C.I.8256 has replaced Osiris as the donor parent of gene system (iv), due to the consistently poor agronomic performance of segregates from crosses involving Osiris.

These research investigations have also shown that five of the resistance gene systems, (i) to (v), involve a single locus on chromosome 3, which implies that resistance from two sources cannot be combined in a single variety. Hence current work is directed towards the resolution of the ultrastructure of this locus, and to the identification of more resistance genes from a wider range of varieties.

However, whilst race-specific ('major gene') resistance may be valuable in the short term, the variation potential of the pathogen is likely to enable it to overcome all possible resistance genes eventually. In the long term, therefore, only non-race-specific resistance is likely to provide a permanent means of control. The efficient

utilization of this form of resistance has necessitated extensive preliminary studies, which are now well advanced.

Results show that non-race-specific resistance to R. secalis can be assessed quantitatively in large field plots and in precise glasshouse experiments, but that there can be considerable variation in field trials using microplots. The use of microplots is essential for early-generation selection, where there are numerous segregates but very limited seed supplies, and so current work is aimed at devising a technique for manipulating this material in order to obtain the optimum expression of resistance. It has been shown that the interaction between plots can be greatly reduced by alternating them with either wheat buffer plots where heavy infections are anticipated (e.g. in winter barleys), or with spreader plots of a susceptible variety where light infections are expected. A uniform inoculation at the seedling stage, either by scattering infected straw or spraying a spore suspension, has also been found useful in reducing error and improving differentiation.

It has also been shown that a useful range of variation in non-race-specific resistance exists amongst the adapted spring barley varieties. Six parent varieties have been crossed in all combinations in order to study the inheritance of this resistance, and to determine whether a level of resistance sufficient for further breeding work can be recovered from this gene pool, thus avoiding recourse to exotic germplasm.

(iii) Brown rust (Puccinia hordei) and yellow rust (P. striiformis)

Recent co-operative Ministry of Agriculture/N.A.A.S. surveys show that barley brown rust and yellow rust are widespread in their occurrence and may be severe in certain situations. This is particularly true of brown rust which in severity and prevalence on barley is second only to mildew. Results of nursery assessments and fungicide trials suggest that rust infection can seriously limit the full expression of yield potential. This may be particularly true for genotypes resistant to the other major foliar pathogens. Consequently, following the appointment of B.C. Clifford to the staff in 1968, rust resistance breeding and research investigations have expanded considerably. The major emphasis is on the development of improved genotypes resistant to brown and yellow rust. However, with the emphasis on non-race-specific resistance, which does not confer complete rust protection, the role of systemic fungicides in the enhancement of such resistance is being investigated. Together these systems may provide an opportunity for the full use of integrated control measures.

As far as race specific resistance to barley brown rust is concerned, a crossing programme has been initiated, making use of the selections Cebada Capa and Estate together with other sources of resistance.

The results of the 1968 National Physiological Race Surveys showed that five major race groups could be distinguished from British isolates by their reaction to eleven differential varieties. These were selected on the basis of their known or postulated genetic constitution from the north American set of Levine and Cherewick (20) together

with other resistance sources which are currently being used in European programmes. Consequently the differentials allow an international interpretation of races and also give specific information relating to material in current use in Europe (Table 9).

Table 9. Barley differentials used in the brown rust physiologic race survey (1968)

C.I. No.	Differential	Gene	Authority
1257	Bolivia	Pa_2 Pa_x	Roane and Starling (22)
5051	Reka 1	Pa_2	
1024	Quinn	Pa_2 Pa_5	
6489	Sudan	Pa	
1145	Gold	Pa_4	
6481	Egypt	?	
3410	Estate	Pa_3	Henderson (12)
3391	Batna	C.I. 935 locus	Starling (24)
935	Peruvian	Pa_2 locus	
6193	Cebada Capa	1 dom. gene	
6306	Ricardo	Pa_2 + ?	Henderson (12)

The varieties Cebada Capa and Estate were highly resistant to all survey cultures tested. The International and European Barley Disease Nursery entries were screened in the glasshouse, and nine genotypes were found to be highly resistant to the major race groups at the seedling stage.

Barley yellow rust presents a less complicated race picture at present. The variety Bigo, which is highly resistant to both race 23 and 24, is being used as a parent in hybridization to develop resistant adapted genotypes.

Turning to non-race-specific resistance, the type of approach that was initiated by B.C. Clifford with crown rust in the United States is being continued at the Station, and expanded to include brown rust and yellow rust. The objectives of this approach are to:-

(a) isolate genotypes which, although susceptible, develop rust slowly during the season ("slow rusters");

(b) distinguish "slow-rusting" from tolerance which is the ability to endure severe rust attack, and

(c) investigate the genetic and physiological basis of these characters.

Genotypes were studied in special rust nurseries in the field in 1968 and 1969 under conditions of relatively uniform inoculum. Some genotypes showing the slow rusting character in both years are given in Table 10.

Information regarding the epidemiology of yellow rust on genotypes varying in their degree of non-race-specific resistance was obtained from a field experiment sown in 1969. The development of barley yellow rust (race 23) epidemics from centrally inoculated foci in circular field plots of Kenia, Union and Domen was studied (Table 11).

Table 10. Slow rusting genotypes of barley and oats

Barley (*P. hordei*)	Barley (*P. striiformis*)	Oats (*P. coronata*)
Vada	Gondar	Arkansas 674
Manchuria	Vaughn	H.B. 72
Monte Cristo	Cebada Capa	C.I. 4763
C.I. 5867	Vantage	Purdue 5112 A1-130-3-1P-1-1
C.I. 3211	80-TT-29	Purdue 4917 A3-31-2
C.I. 9978	C.I. 2377	Purdue 461 A1-8-2-2

Table 11. Spread of *P. striiformis* in circular plots (dia. 4.88 m) of barley

Variety	Race	Distance from plot centre (m)†				
		0	0.6	1.2	1.8	2.4
		Per cent flag leaf infected				
Kenia	23	10.8	2.2	0.8	0.3	0.2
Union††	23	12.6	3.7	2.0	0.9	0.8
Domen	23	28.8	14.7	8.3	4.1	3.1
Domen	24	17.5	7.2	2.2	1.0	0.9

† Average of 8 equally spaced sampling points at each distance, 4 replicates
†† 3 replicates

Rust spread was greatest in the Domen plots, intermediate in Union and least in Kenia, reflecting the relatively slow rusting character of Kenia and Union. In a subsidiary study, race 24 or *P. striiformis* spread more slowly on Domen than race 23, indicating that race 24 was relatively less aggressive under these conditions of host and environment (Plate 2).

Studies of the mechanisms of slow rusting and genotype evaluation have been greatly facilitated by the use of a settling tower similar to that described by Eyal, Clifford and Caldwell (2), for quantified inoculation of cereal plants.

Systemic fungicide trials with the 1, 4 oxathiins, 'Plantvax' and 'Vitavax', indicated that the former is effective in the control of barley brown rust, barley yellow rust and oat crown rust when applied as foliar sprays at the tillering and heading growth stages. In a trial where Plantvax was applied as a 2% seed dressing, the slow rusting character of Proctor, Kenia and Union was further enhanced indicating the value of integrating these control measures.

The above data, together with other information, suggest a plausible theoretical

Plate 2. Circular plot of a barley cultivar being assessed for rate of spread of disease from a central focus.

Table 12. Comparison of grain yields of resistant and susceptible barley genotypes on cereal cyst nematode infested soils (collaborative NAAS/WPBS trials)

N.A.A.S. Officer concerned with trial	Site	Year	Yield kg/ha R	S	% R/S
T.Glyn Davies (Bangor)	Ruthin (Ty'n Llanfair)	1967	4717	4516b	104.4
	Ruthin (Glan Hespin)	1969	3738	3688b	101.3
C.A.Collingwood (Reading)	Damerham, Hants.	1967	2308	2032b*	113.6
	Damerham, Hants.	1968a	2960	2960	100.0
R.Gair (Bristol)	West Lavington, Wilts	1967	5381	5105b*	105.4
	Kingston Deverill, Wilts	1967	2898	2910b	99.5
	Kingston Deverill, Wilts	1968a	3989	3374b*	118.2
L.E.W.Stone and C.W.Graham (Reading)	Overton, Hants.	1969	4880	4390c*	111.1
	Eaton, Berks	1969	4127	3864c*	106.8
M.E.John (Shardlow)	Southwell, Notts	1969	5218	5620b	92.9
W.P.B.S.	Ruthin (Glan Hespin)	1965	5896	4930b*	119.6
-	" "	1966	4855	4428b*	109.6
-	" "	1967	5682	5507b	103.2
-	" "	1968	4666	4491b*	103.9
-	" "	1969d	3073	2722b	112.9
Mean of all trials			4293	4036	106.6

* differences significant at P = 0.05

a resown on 1967 plots

b comparison with near isogenic susceptible genotypes

c comparison with susceptible Zephyr

d after four years of continuous resistant or susceptible genotypes

model for the integrated control of barley yellow rust. As far as is known, two races of P. striiformis exist on barley. Several current varieties, e.g. Zephyr and Cambrinus carry specific resistance to race 23, thus causing a pressure for the selection of race 24. This latter race appears to be less aggressive, which should cause a reduction in the rate of build-up. Furthermore, other varieties, such as Proctor and Kenia, develop yellow rust relatively slowly (non-specific resistance), so the use of these varieties further reduces the rate of rust build-up. Finally, seed treatment with Plantvax may be economically feasible on slow rusting varieties, thus further reducing the rate of rust increase. Therefore, the integrated use of race-specific resistance, non-race-specific resistance and a systemic fungicide may together provide a method of giving stable control of P. striiformis.

(iv) Cereal cyst nematode (Heterodera avenae)

During the development of the cereal cyst nematode resistant Sabarlis, near isogenic populations of barley, which differ only in respect of the single gene Ha, were produced. This gene confers resistance to pathotypes 1 and 2 of the nematode. These isogenic populations have made possible an objective assessment of the effects of the nematode on barley yields. In trials on cereal cyst nematode-free sites, and on infested sites treated with nematicides to remove the effect of the nematode, these resistant and susceptible lines have consistently given similar yields. However, trials on infested land, conducted at Ruthin in North Wales by J. Cotten and at other sites by cooperating members of the N.A.A.S. Cereal Nematodes Working Party, show that an average yield reduction of 6-7% occurs in susceptible barley due to the effects of the nematode (Table 12).

The resistance conferred by the gene Ha retards development of the larvae within the roots of the host, and none or very few females become adult in resistant plants. The effect of repeatedly growing resistant genotypes on infested land is the depression of the nematode population. R. Gair (personal communication) using the resistant barley genotypes developed at the Welsh Plant Breeding Station, has demonstrated the value of repeatedly cropping with these genotypes on an infested site in Wiltshire, thereby reducing the nematode population and increasing yields still further (Table 13).

Table 13. The status of cereal cyst nematode populations in heavily infested soil, and yield of grain after cropping with resistant and susceptible genotypes of spring barley (R. Gair, pers. comm.)

Nematode reaction of barley genotypes	Cereal cyst nematode eggs/g of soil		Grain yield 1968 kg/ha
	Post-cropping 1967	Post-cropping 1968	
Resistant	15.4	6.84	3989
Susceptible	49.9	21.2	3374

On field plots at Ruthin which had grown either cereal cyst nematode resistant or susceptible barleys continuously for three years, large numbers of migratory plant parasitic nematodes were found in addition to Heterodera avenae. The most abundant of these was Pratylenchus minyus.

The extent of the root invasion of a following crop of Proctor barley (Table 14) indicates that both cereal cyst nematode and migratory nematodes were more prevalent on those plots which had previously grown susceptible barley. This suggests that there was no competition between the different nematode species.

Table 14. Numbers of nematodes/g of root after growing cereal cyst nematode resistant and susceptible barley genotypes at Ruthin

Nematode species	Previous barley crop reaction to H. avenae	Sampling date		
		9 May 1968	10 June 1968	9 July 1968
H. avenae	Resistant	6.2	0	0
	Susceptible	112.5	50.0	6.2
Migratory nematodes	Resistant	1837.5	556.2	337.5
	Susceptible	2462.5	737.5	387.5
SE for migratory nematode means		±809.79	±162.08	±86.90

Even with such heavy infestations, there was no obvious effect on crop growth which could be attributed to the migratory nematodes.

Wheat

1. Spring wheat breeding

There has been no extensive breeding programme for wheat in the Department, the limited programmes that have been undertaken were concentrated on the development of early maturing non-shattering lines suitable for western conditions. No new varieties of sufficient merit to include in National Trials have yet emerged from this work, partly because they have not outyielded the current improved varieties emanating from other sources and partly because the breeder (D. A. Lawes) has not yet located sufficiently good sources of resistance to Septoria spp for incorporation in the breeding programme. Glume blotch (caused by S. nodorum) is claimed to be the prime cause of grain shrivelling in wheat and there is no doubt that this inadequate filling of the grain is an important factor in preventing the wheat crop realizing its full potential in the western half of Britain.

2. Glume and leaf blotch (Septoria spp.)

In order to develop a method which will enable genotypes to be efficiently screened for resistance to Septoria nodorum and S. tritici, a joint project has been undertaken with the U.C.W. Department of Agricultural Botany, and a suitable technique to artificially inoculate ears of wheat in the field has been developed by B.M. Cooke, a postgraduate research student at the University. In 1968 inoculated ears of Opal and Svenno spring wheat indicated a grain yield reduction of 20% due to S. nodorum and 9% due to S. tritici.

The yield component most significantly correlated with severity of disease infection was grain size. Table 15 presents data for the mean effect of both diseases on these two varieties at different levels of inoculum. Although S. tritici at the highest intensity produced some grain shrivelling, the effect was not as marked as with S. nodorum.

Table 15. Effect of different levels of spore inoculum of S. nodorum and S. tritici on mean grain size of Opal and Svenno spring wheat

Inoculum level (spores/ml)	1,000 grain wt (g) S. nodorum	S. tritici
0	33.8	34.8
10^3	33.7	35.9
10^4	33.3	33.2
10^5	31.8	33.0
10^6	29.0	33.9
10^7	27.2	31.7

S. tritici was significantly less harmful than S. nodorum on Svenno as compared with Opal.

A further experiment, comparing the effect of Septoria disease on the yield of 15 varieties of diverse origin, indicated that some genotypes were less susceptible than others, although no real resistance was revealed. The examination of further genotypes alleged to exhibit resistance is being continued. Meanwhile, initial crosses have been made between the most promising material screened and adapted varieties, with a view to developing lines with an enhanced level of resistance.

Field beans

1. Review of general breeding objectives

The aims of the field bean (Vicia faba L.) breeding programme being conducted by D.A. Lawes are to improve the yielding capacity of the crop and the reliability with which such enhanced yield is produced.

Reliability of yield is affected by environmental hazards which limit the development of the crop or cause loss of the grain before it can be harvested. Examples of factors which may be seriously limiting bean yields are winter killing in winter beans, chocolate spot disease and aphid attack. Unfortunately, good genetic resistance to all these agents still remains to be found. Some success has been achieved in improved winter hardiness by the development at the Station of the new variety Daffa which has done well in national trials, being on the current N.I.A.B. recommended list of winter bean varieties. It is especially recommended for western conditions where it has shown good winter survival.

Besides limiting factors of this category, however, a large part of the unreliability of yield is due to factors which affect pollination, seed set, and seed development. The present field bean crop is partly self- and partly cross-pollinating, and a degree of cross-pollination is necessary to ensure reasonable yields. This cross-pollination is accomplished by long tongued bumble bees, and it is the inadequacy of bee activity in certain climatic conditions which is one of the reasons that yields are unreliable.

One method of improving yields in cross-pollinating crops is the exploitation of hybrid vigour, but because this still relies on bee activity to carry out the necessary cross-pollination, the fundamental problem of seasonal variation is not resolved.

The alternative scheme, and that which is the major project in the bean improvement programme at the Station, is to convert the crop into a self-pollinating one. If successful, bee visitation would not be essential and seed setting could continue irrespective of the external conditions. The activity of the bee population in the harvest year, and the degree of hybridity in the crop arising from cross-pollination which occurred during preceding generations, would not be of overriding importance.

Such conversions to self-fertility have already occurred naturally in several species during the course of domestication from wild forms; tomatoes and garden peas are just two examples. There is now sufficient evidence from our work to indicate that this conversion should be possible with field beans in relatively few generations.

2. Progress in developing inbred lines

Results of experiments have indicated that there are several aspects of self-fertility to be considered. As it is intended to forgo bee visitation, the flowers must be self-tripping, so that the mechanical operations carried out by the bee become unnecessary, and pollen transfer and fertilization occur unaided (22). The ability to self-trip is a highly heritable character, and its genetic control follows a dominant model (7). When self-tripping has been established, the other aspects of self-fertility, termed autofertility, can be incorporated. The factors controlling this are mostly inherited according to an additive model, and are not widely influenced by environmental factors (6).

In 1962 and 1963 a collection of bean varieties from all parts of the world was screened in the glasshouse both for the ability to self-trip and for auto-fertility. Of

these less than twenty were selected for further observation and utilization as parents in breeding programmes designed to produce commercial varieties of self-fertile beans. Since that time, additional accessions have been tested as they became available and the best had been brought into the programme.

Exotic varieties, and in particular Rahria Sem from New Delhi (Ch 182), have proved to be the best source of characters essential to self-fertility, but agronomically the exotic types are totally unsuited to European conditions. The breeding material, therefore, emanates from selections covering a wide range of variation including types from widely differing geographical areas and varying in plant and seed characters (broad, horse and tick beans).

Since the breeding programme was commenced, it has been based on recurrent selection accompanied by assortative mating. At each stage, selection has been made for seed setting under bee-proof conditions; this selection therefore combines the attributes of ability to self-trip, auto-fertility and potential yield. The latter includes selection away from any inbreeding depression. Concurrently, a small quantity of seed of the most promising lines is grown in the field so that agronomic performance can be assessed and also so that seed can be multiplied for field yield trials. Data from the field observations have considerable bearing on the selection of comparable lines to be continued in the bee-proof glasshouse for subsequent stages.

The largest part of the testing of early generation material in field trials has been carried out at Aberystwyth, but material has also been tested at the N.I.A.B. subcentre at Seale Hayne Agricultural College, Devon, since 1967.

Considerable success has been achieved in increasing the degree of self-fertility, and grain yields of up to 80% of outpollinated control varieties of spring beans have been obtained. Bearing in mind the totally unadapted nature of some of the parents used, and the relatively low selection pressure exercised so far for agronomic performance in order to maintain a wide genetic base, these yield results are encouraging. Selection amongst this material continues and some lines have re-entered the breeding programme as parents.

Self-fertility is being given priority in this project, but once self-fertility and yield have been established, other important attributes will be incorporated which will improve the suitability of field beans for sowing and harvesting with the present cereal crop machinery. The breeding material includes variation for such characters as short haulm, determinate growth, early ripening of seeds and early plant senescence, small seeds and non-shattering pods. These characters combined in the one self-fertile variety would provide an attractive break crop for highly mechanized cereal growers.

Brassica crops

The brassica crops have received little attention from the breeder and research worker in the past. Most varieties in existence are variable and have been developed

by mass selection techniques and visual assessment. Since the brassica work was initiated at the Station in 1955, T.D. Johnston has devoted his attention to the breeding of improved types and to investigations into the genetic control of important characteristics of the crop.

1. Kale breeding and development of hybrids

It has been found that some components of yield exhibit marked heterosis in crosses among inbred lines, and that the level of heterosis is greater in crosses among inbred lines derived from distinct varieties (13, 14). This was confirmed in a yield trial in 1969 of double-cross hybrids between inbred lines of dwarf thousand headed kale and a leafy French type (Chou branchu du Poitou). In this trial the mean leaf yield of the inter-varietal hybrids was 4940 kg/ha compared with 3530 kg/ha and 4230 kg/ha respectively for the pooled populations of intra-varietal double-cross hybrids derived from the same sets of inbred lines.

Tests of the individual double-cross hybrids of dwarf thousand headed kale against the parent variety in another trial indicated a mean 10.0% dry matter yield advantage for the hybrids. Investigations are proceeding into large scale production of the best of these hybrids and at the same time into the production of a synthetic variety based on a small number of inbred lines including those used above. The synthetic, if comparable in agronomic value, would be preferable to a double-cross hybrid because of the relative simplicity and cheapness of seed production.

Similar investigations in a marrow-stem kale (MSK) x kohlrabi single-cross population from other selected MSK inbred lines gave a higher total yield than Maris Kestrel, but was less leafy and more fibrous in the lower stem. Yields of the various types in the trial are shown below as percentages of Maris Kestrel.

Variety	Yield of leaf	Yield of stem	Stem length
Maris Kestrel	100	100	100 (= 970 mm)
Commercial MSK	63	140	155
MSK double-cross	92	142	130
MSK x Kohlrabi single-cross	107	83	55
(MSK x Kohlrabi)F_7	71	97	83

The (MSK x Kohlrabi) F_7 generation is a mass selection and has consistently exhibited high stem quality but lacks sufficient yield capacity to merit further investigation.

N.I.A.B. trials with other Station selections, namely Da 141 (semi-dwarf thousand headed kale) and Da 154 (marrow-stem kale) have indicated that their superiority over existing commercial types is marginal and hence further tests are needed.

Studies have been carried out on the effects of plant spacing and fertilizer treat-

ment (nitrogen) on contrasting genotypes of marrow-stem kale, with particular reference to their effect on individual components of yield, and possible genotype/environment interactions. The three varieties chosen were Maris Kestrel, a very leafy type with low stem yield, and two other commercial stocks, one with high stem yield and low leaf yield, and the other which showed intermediate expression of these characters.

The results showed that leaf number per plant was unaffected by fertilizer but responded strongly to spacing. Leaf size responded to both factors, but most markedly to increased spacing. Their product, i.e. leaf yield, showed a steady increase in response to nitrogen with no environment/variety interaction, but the response to spacing showed interaction in that Maris Kestrel exhibited a steady increase in leaf yield from the closest to the widest spacing, whereas the total yield of leaf per unit area of the other two varieties decreased with reduction of plant population. Stem yield per ha exhibited marked and uniform increase due to fertilizer, and a uniform decrease due to reduced density through only partial compensation by increased size of each stem.

2. Physiological investigations with kale

Assessments of net assimilation rate of various kale genotypes have been made by measuring dry weight gain of detached leaf disks after a standard exposure to light in the laboratory. Dry weight gains of the order of 3-4% per hour equivalent to approximately 10 mg/dm^2 of leaf surface per hour were obtained, which compares well with published results of similar investigations on other species.

A test using three inbred lines of marrow-stem kale and their F_1 hybrids showed a small mean superiority of 3.6% to the hybrids in terms of assimilation per unit area. There was also evidence of inbred-line genotype differences.

In the breeding programme the ability to store pollen of early flowering for use on later flowering plants or in the following season, could be useful. In May 1968 freshly burst anthers of various B. oleracea genotypes were collected in the glasshouse. They were dried immediately over calcium chloride at $+2^{o}C$ for 24 hr, sealed into small specimen tubes and stored in a refrigerator. In March 1969 the stored pollen was used immediately after removal from storage to bud-pollinate plants of different cultivated types. Satisfactory seed set was obtained in each pollination and the progenies when grown on were of the hybrid type expected. Thus this very simple technique proved adequate for season-to-season storage and with refinement should facilitate storage of pollen for a considerably longer period.

3. Rape breeding

The primary aim of the programme is to improve the yield of the crop. Various crossings and selections have been made for a number of years but have not led to the isolation of markedly superior types except for the development of the clubroot resistant variety Nevin.

Extensive Station and N.I.A.B. trials have established that under disease-free con-

ditions the yield of Nevin is closely similar to that of other forage rapes. On disease-infested land, however, it outyields susceptible types by a substantial margin and in view of the widespread occurrence of the disease, efforts are now being concentrated on the development of higher yielding varieties carrying the Nevin resistance factors. However, in some situations Nevin can succumb to severe infection with clubroot.

The variation in reaction of Nevin to clubroot is due to the existence of distinct pathogenic races of Plasmodiophora brassicae. The existence of three races, one of which is pathogenic to Nevin, has already been reported from the Station (15). A fourth race designated N4 has now been isolated. Both parents of Nevin and Nevin itself are resistant to this race, but commonly grown commercial strains of forage rape and all oil rapes so far tested are susceptible. However, within forage rape stocks a very small percentage of resistant plants may be present. This resistance has now been shown to be conditioned by a single dominant gene, and a population homozygous for this resistance factor only is now being developed for addition to the stock of available differential genotypes which are shown below with their reaction to the four races.

Differential genotype		Reaction to race			
		N1	N2	N3	N4
Commercial giant rape	Dc 119	+	+	+	+
Selection from above	Dc 128r	+	+	+	-
New Zealand rape	Dc 129	+	-	+	-
Wilhelmsburger swede	Dc 130	-	+	+	-
Nevin rape	Dc 101r	-	-	+	-

+ = Susceptible; - = Resistant

In the swede there is an urgent need for disease resistant varieties well adapted to British conditions. Lines carrying the resistance factors against clubroot races N1, N2 and N4 have been developed and are undergoing final selection for uniformity and resistance before replicated yield trials. These lines have given disease-free crops in the heavily infected clubroot nursery at the Station, and are of the purple top type with globe or short tankard shaped roots (Plate 3).

4. Resistance to mildew (Erysiphe cruciferorum) in swedes

Single plant selections from an introduced variety of swedes show consistently less infection by the disease in the field and on artificially inoculated detached leaf segments floated on benzimidazole in the laboratory (Table 16).

The assessment of mildew infection presents difficulties because of the diffuse nature of growth of the pathogen. Nevertheless, there is reasonable correspondence between the two methods of assessment.

Preliminary investigations indicate that the resistance is polygenically controlled,

Plate 3. Club root Plasmodiophora brassicae. Susceptible cultivar (top) and resistant segregate (bottom) of swedes grown on infested land. The resistance factors effective against club root races N_1, N_2 and N_4 have been introduced from Nevin rape Dc 10lr.

Table 16. Mildew infection scores of swede varieties and inbred line selections after natural field infection and on artificially inoculated detached leaf segments

Genotype	Mildew score Field	Mildew score Segments
Broadland (Dc 118)	10†	48††
Pentland Harvester (Dc 120)	10	70
Dc 94 Selection A	4	18
Dc 94 Selection B	7	35
Dc 94 Selection C	6	28
Dc 94 Selection D	6-7	38

† Scores 0-10, 10 = all lower leaves heavily infected
†† Estimated % cover; mean of 8 segments from four plants

and since the lines carrying the resistance are very unsatisfactory in other respects, the incorporation of this resistance into well adapted genotypes will be a long term procedure. An alternative method of control is the use of fungicides. Tests with a systemic fungicide have shown that good control of the disease can be obtained, but dose rates are at present uneconomically high. The same fungicide (PP675) has, however, proved extremely valuable in preventing the build up of the disease on breeding plants in the glasshouse which, especially towards the end of the crossing season, can become so severely infected that only poorly developed seed is produced.

5. Fodder radish

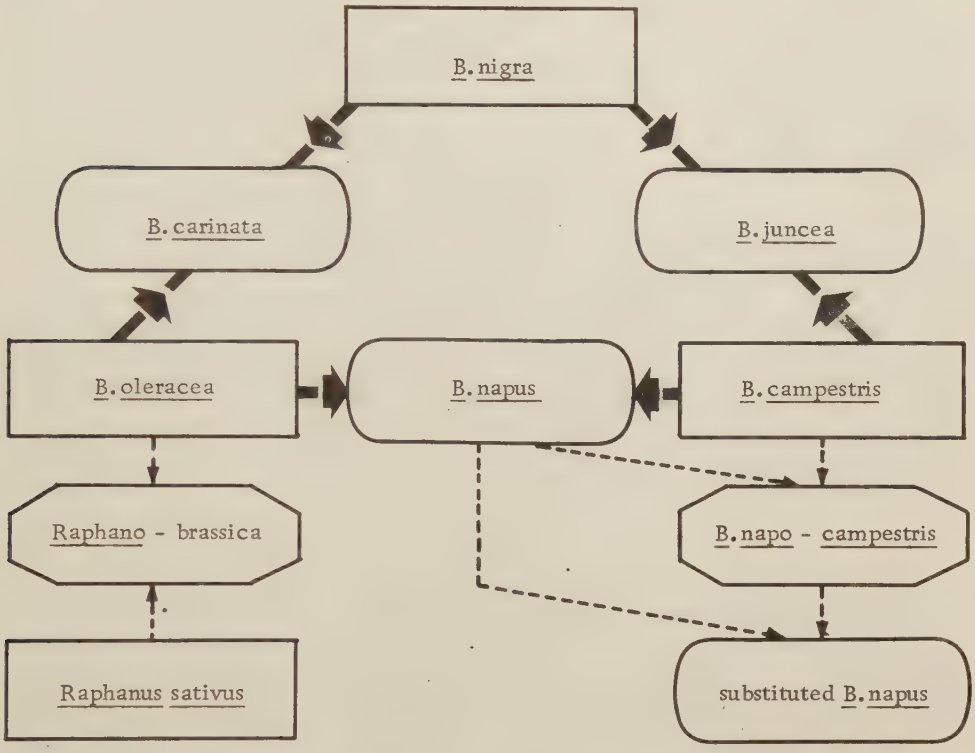
The agronomic potential of a possible alternative to rape, the fodder radish (Raphanus sativus), has been tested extensively at the Station. The aspects of management necessary to ensure good crops have been established and it has been found possible to consistently produce high yields of digestible dry matter superior to rape sown at the same time. It also exhibits a high level of disease resistance. The main disadvantages of the crop are tendency to flower within a few weeks of sowing and lack of winter hardiness. Two selections Df 5 (diploid) and Df 10 (tetraploid) have been produced. In trials they have shown the same ability to produce a large bulk within a short time of sowing, but are significantly later flowering and thus have a more extended period of suitability for grazing.

6. Interspecific studies

The radish is also being used in interspecific hybridization with B. oleracea. The opportunities for interspecific hybridization in the Brassiceae are quite numerous and may be grouped into three categories namely (1) the synthesis of amphiploids closely similar to natural amphiploids such as B. napus, (2) the synthesis of unnatural amphiploid or other genome combinations, (3) interspecific hybridization as a step in the transfer of desirable units of genetic material from one species to the other. These possibilities are illustrated in the following diagram (Fig. 3) which shows the inter-

relationships of the three basic species B. oleracea, B. rapa and B. nigra with their naturally occurring amphiploid hybrid derivatives, together with other aspects of interspecific hybridization being investigated at present.

Fig. 3



The investigations into the synthesis of the hybrid between B. oleracea and R. sativus are being pursued with the object of combining the favourable attributes of the former, namely hardiness and biennial habit, with the rapidity of growth and disease resistance of the latter to produce a new crop probably as an alternative to forage rape.

At the diploid level, bud pollination of the radish without emasculation led frequently to the production of up to five embryos per pod with only 0.5% matromorphous plants in 1968, and about the same quantity in 1969. Shrivelling of the embryos at a late stage of development is common due to drying out after bursting of the testa by the apparently excessive development of endosperm in these hybrids. This is overcome by excision of the embryos and transplantation direct into sterile compost as soon as the pods exhibit the first signs of maturation.

Initially, hybrids were made by crossing early and late maturing varieties of radish with various kale types. The influence of the parental genotypes was apparent in the diploid F_1 hybrids. Hybrids of radish with kales which have a relatively low vernalization requirement tended to flower in the autumn of the season of production, but those involving dwarf thousand headed kale appeared to have a definite cold induction re-

quirement. Furthermore, the latter hybrids were shorter, more branched, leafier and more winter hardy than those in which marrow-stem kale was the male parent.

Consequently, efforts are now being concentrated on hybrids of radish with dwarf thousand headed kale. Colchicine treatment of seedlings or axillary buds induced into activity by main shoot decapitation has given many plants with the typical morphological features of tetraploidy, confirmed in a few cases by chromosome counts and apparently fertile pollen. However, fertile F_2 amphiploids have not yet been produced on these plants.

The other aspect of interspecific hybridization being pursued is an attempt to transfer factors for resistance to certain races of clubroot from B. rapa to B. napus. The initial hybridization using B. napus as female parent is readily performed and the hexaploid AAAACC genome is induced by colchicine treatment. The hexaploid itself may constitute a worthwhile crop and is being tested, but also attempts are being made by backcrossing to B. napus to return to the AACC genome with substitution of the desirable attributes from B. rapa. F_1 hybrids of the cross Nevin with a turnip introduction have shown resistance to all four races of clubroot including race N3 to which no known resistance exists in B. napus.

FUTURE DEVELOPMENTS

As a consequence of the Introduction of the Plant Varieties and Seeds Act of 1964 and the granting of plant breeders rights, we can confidently expect private breeders to expand their efforts and produce new varieties of the more popular arable crops to satisfy the immediate needs of the farmer. Consequently the Department will be able to devote more effort to research into more fundamental and long term problems of crop improvement, whilst continuing to give a lead in developing techniques for producing new varieties. There will be need for very close collaboration between breeders, both state-aided and private, to avoid unnecessary duplication. The solving of many of these problems will require the closest collaboration with research workers engaged in other scientific disciplines.

The reduction of yield losses due to disease will receive top priority in the work of the Department. In an area with a mild humid climate such as Aberystwyth, field conditions are ideal for the development of air-borne disease. These high stress conditions enable the breeder to select efficiently genotypes with various types of resistance. In addition, the absence of large areas of winter sown cereals in the vicinity provides an opportunity for controlling the initial levels of air-borne inoculum. The genetic basis of race-specific and non-race-specific resistance mechanisms to various pathogens will be elucidated, and the epidemiological significance of introducing varieties with increased non-race-specific resistance into practice will be assessed. Moreover, investigation will be made of the possibilities of developing genotypes better able to absorb and translocate systemic chemicals which might be used to protect the crop.

Experiments will be continued to provide better knowledge of the genetic systems

controlling characters of economic importance, especially those which enhance the full expression of yield potential under the more hazardous conditions for harvesting encountered in the western half of Britain. Methods will be developed to apply the physiological techniques to the identification of the components influencing high biological efficiency. A new approach to breeding for maximum yield and quality in cereals and other arable crops would then be possible. Furthermore, recently developed statistical techniques will facilitate the study of quantitative variation, the handling of genotype x environment interactions and the calculation of meaningful selection indices using the facilities for complex calculations offered by the electronic computer. These will aid greatly in the early generation selection of the most promising material in breeding programmes.

More effort will be concentrated on devising new methods and improving existing techniques of introducing alien species variation into the oat and brassica crops by chromosome manipulation, and on assaying the contribution to yield of individual chromosome segments. The levels of heterosis obtained in inbred cereals will be assessed and the feasibility of its exploitation will be determined. On the other hand, in beans, because of the frequent absence of pollinating agents at the critical time of flowering under conditions prevalent in western Britain, it will be difficult to harness F_1 hybrid vigour, and consequently efforts are being made to convert the bean into a self-fertilizing crop.

With the close collaboration of the breeder, chemist and animal nutritionist it should be possible to increase the nutritive value of all the cereals, but in particular of oats, by increasing the oil content and improving the digestibility of the grain. In addition, there is great scope for improving the protein and essential amino acid content of the grain. Of particular importance in western Britain, where arable crops are mainly grown on livestock farms, it will be necessary to constantly bear in mind the nutritive value of the whole crop.

Other advances may come, but are not forseeable with any precision. Interesting developments in the fields of mass production of haploids, gene incorporation, mitochondrial complementation, etc. all present opportunities which must be investigated fully in order to ascertain whether they can be used by the plant breeder.

As with all other crops, the ultimate goal of the arable crop breeder is to improve the genetic pattern of his plants in relation to their economic use. The rate of progress in the future will depend to a large extent on his ability to harness and integrate the products of fundamental research from many different fields of biology into superior genotypes well adapted to their environment and suited for intensive cultivation.

References

(1) J.Cotten, 1967, Ann.appl.Biol. 59, 407-413.

(2) Z.Eyal, B.C.Clifford and R.M.Caldwell, 1968, Phytopath. 58, 530-531.

(3) D.J.Griffiths, J.W.Holden and J.M.Jones, 1957, Ann.appl.Biol. 45, 709-720.

(4) D.J.Griffiths, 1958, Trans.Br.Mycol.Soc. 41, 373-384.
(5) D.J.Griffiths, D.G.Rowlands and W.T.H.Peregrine, 1959, J.agric.Sci., Camb. 52, 189-199.
(6) A.S.Hanna and D.A.Lawes, 1967, Ann.appl.Biol. 59, 289-295.
(7) A.S.Hanna and J.D.Hayes, 1968, Z.PflZucht. 60, 315-326.
(8) J.D.Hayes, 1960, Agriculture, Lond. 67, 277-281.
(9) J.D.Hayes, 1965, Ph.D.Thesis, Univ.Wales (unpublished).
(10) J.D.Hayes, 1968, Euphytica 17 (1968 Suppl.1) 87-102.
(11) J.D.Hayes and J.Cotten, 1969, Proc. 2nd Int. Barley Genet.Symp.,Pullman, Washington State, U.S.A.
(12) M.T.Henderson, 1945, Ph.D.Thesis, Univ.Minnesota (unpublsihed).
(13) T.D.Johnston, 1963, Euphytica 12, 198-204.
(14) T.D.Johnston, 1968a, Euphytica 17, 63-73.
(15) T.D.Johnston, 1968b, Pl.Path. 17, 184-187.
(16) E.T.Jones, 1941, Genetica 22, 419-434.
(17) I.T.Jones and J.D.Hayes, 1967, J.agric.Sci., Camb. 69, 103-109.
(18) I.T.Jones and J.D.Hayes, 1968, J.agric.Sci., Camb. 70, 405-410.
(19) D.A.Lawes and J.D.Hayes, 1965, Pl.Path. 14, 125-128.
(20) M.D.Levine and W.J.Cherewick, 1952, U.S.D.A.Tech.Bull.No.1056.
(21) T.Rajhathy, F.J.Zillinsky and J.D.Hayes, 1966, A collection of wild oat species in the Mediterranean region. Ottawa Res.Stn Can.Dep.Agr. 3-25.
(22) C.W.Roane and T.M.Starling, 1967, Phytopathology 57, 66-68.
(23) D.G.Rowlands, 1955, Agric.Progr. 30, 137-147.
(24) T.M.Starling, 1955, Ph.D.Thesis, Iowa State Coll.
(25) 1966 Welsh Pl.Breed.Stn Report for 1965, p.38

DEVELOPMENTAL GENETICS

J.P. COOPER

The grass crop is grown to provide digestible energy and other nutrients for the ruminant. This Department is therefore concerned with the efficiency with which the crop converts the seasonal input of solar energy and soil nutrients into a form most suitable for the animal, and with the possibility of increasing this efficiency by selection.

The experimental sequence adopted has been to identify those physiological and biochemical features of the grass plant which determine its efficiency of energy and nutrient conversion, to measure the amount of genetic variation available for these characteristics and to assess its potential use in a selection programme.

The topics currently under study include:-

1. The photosynthetic activity of the individual leaf or young seedling, including biochemical variation in the main enzyme systems controlling photosynthesis;
2. The pattern of light interception by the canopy, as influenced by leaf arrangement and by the reflectivity and transmissivity of individual leaves;
3. The biological potential of an established sward, when water and soil nutrients are not limiting;
4. Response to, and uptake of soil nutrients, especially nitrogen, phosphorus and potassium, including biochemical variation in the relevant enzyme systems.

ANALYSIS OF PRODUCTION CHARACTERS 1954-1965

This combined physiological and genetic approach to crop improvement arose out of research started in the Grass Breeding Department of the Station in the late 1940s. From the early days of the Station it had been clear that two of the most important agronomic features which influence seasonal production were maturity date, based on the timing of floral development, and persistency, related to the annual, biennial or perennial habit.

1. Physiological basis of flowering responses in *Lolium*

The physiological basis of these differences in flowering responses was examined in a range of ryegrass varieties, from the extreme annual Westernwolths and Wimmera ryegrasses, through the biennial Italian forms to the extreme perennial varieties, S.23 and S.101. It was found that the degree of perenniality, based on the survival of

vegetative tillers from one year to the next, was closely related to a requirement for exposure to low temperature during the winter, before flowers could be initiated. In the extreme annual Westernwolths ryegrass, as in spring cereals, there was no requirement for cold exposure, and all plants headed rapidly after a spring sowing. In the winter-annual Wimmera ryegrass, floral initiation was accelerated by low temperature, although there was no absolute requirement for cold, but most varieties of perennial ryegrass required varying periods of exposure to cold before flowering could occur, the exposure required being greatest in the most persistent forms. The Italian ryegrasses were intermediate between the annuals and perennials in their flowering requirements (2). This cold exposure could be applied at an early stage to the imbibed seed, and later work showed that short day exposure could, to a certain extent, substitute for low temperature.

Once sufficient low temperature had been given, the initiation and further development of the inflorescence was controlled by photoperiod. All ryegrass plants were long-day in the sense that flowering was most rapid in long days or continuous light, but the early, medium and late flowering varieties differed in their critical day length, all plants of the early flowering Irish ryegrass, for instance, would produce heads in a 12 hr day, whereas the late flowering S.23 required over 13 hr for floral development.

Although the timing of ear initiation in the spring was controlled largely by photoperiod, the subsequent development of the ear and the time of flowering were markedly influenced by spring temperature, and most of the seasonal variation in date of heading at Aberystwyth could be explained in terms of temperature during ear development once the critical photoperiod had been reached. Consequently, later-flowering varieties, such as S.23, showed less year to year variation than the earlier-flowering S.24 or Irish. These effects of spring temperature or date of heading were confirmed by transplant studies in which clonal material of early, medium and late-flowering varieties was grown along a latitudinal cline from Shetland to the Isles of Scilly and an altitudinal range of more than 725 m from Aberystwyth to the summit of Pumlumon. This difference of 725 m in altitude, within 24 km of Aberystwyth, had in fact a similar effect on heading date to the difference of 10° in latitude between Scilly and Shetland. The relative order of early, medium and late-flowering material remained the same at all centres, but the difference between the early and late varieties decreased in the localities with lower spring temperatures.

These flowering responses were closely related to the past agronomic and climatic selection to which the varieties had been exposed. The Mediterranean annual Lolium rigidum, for instance, had been selected in an environment where summer drought was the limiting climatic factor; seeds germinated with the autumn rains, and flowering and seed production had to be completed in spring before the summer drought began. These conditions have selected an annual life cycle with little or no cold requirement and the ability to flower in the short days of early spring. At the other extreme, the more persistent forms of perennial ryegrass, such as S.23, derived from old grazed pastures in Britain have evolved under intensive grazing in which the continued development of vegetative tillers was essential and there was little necessity for reproduction by seed. In these varieties a marked cold requirement for floral induction

and a high photoperiodic threshold has resulted in a high proportion of vegetative tillers throughout the year.

Even so, considerable variation in the quantitative flowering responses to both temperature and photoperiod occurs within these cross-fertilizing ryegrass varieties, and although each variety is fairly uniform in flowering behaviour in the environment under which it had been selected, it often reveals a wide range of variation when grown under altered conditions of temperature or photoperiod (5).

2. Genetic control of flowering responses in Lolium

It was clear that appreciable variation for flowering responses to temperature and photoperiod existed both between and within these contrasting ryegrass populations, so the next step was to investigate the genetic control of these responses, the amount of genetic variation available and its potential response to selection. The inductive response to cold and the photoperiod requirement for floral initiation both proved to be polygenically controlled. and no main genes of large effect could be detected. Each of these cross-fertilizing populations, while phenotypically uniform in its original environment, contained much potential genetic variation. Most individuals in these populations are highly heterozygous and release appreciable variation in each generation by segregation and recombination (3). Such a genetic structure is typical of many cross-fertilizing organisms, such as Drosophila and the mouse, which had been studied more intensively.

The heritability of date of heading, as an index of photoperiod response, was assessed from parent/progeny regression within three contrasting varieties, the annual Wimmera ryegrass, and Irish and Kent perennial ryegrass. In all cases, high heritability values of over 70% were obtained, suggesting that rapid response to further selection should be possible within each variety. Divergent selection for early and late flowering was therefore started within each of the two perennial varieties, Kent and Irish, and continued for seven generations. Back selection lines were established after the first generation, to examine the amount of genetic variation carried within each initial group of four plants of similar heading date.

Response to selection was rapid and continued steadily for the seven generations of the experiment. By that time the early and late selection lines from each variety were discontinuous and well outside the initial range of the variety. In fact, the full range of the early-flowering Irish had been obtained by selection from within the late-flowering Kent ryegrass and vice versa (Fig.1). In the late selection line from Kent ryegrass, a small proportion of non-flowering plants were obtained from the sixth generation onwards. Even after seven generations of selection, the early and late selection lines still contained appreciable genetic variation, and the back selection lines indicated that in this cross-fertilizing species four plants of similar heading date could carry as much potential genetic variation in the heterozygous condition as was expressed phenotypically in the original variety (4).

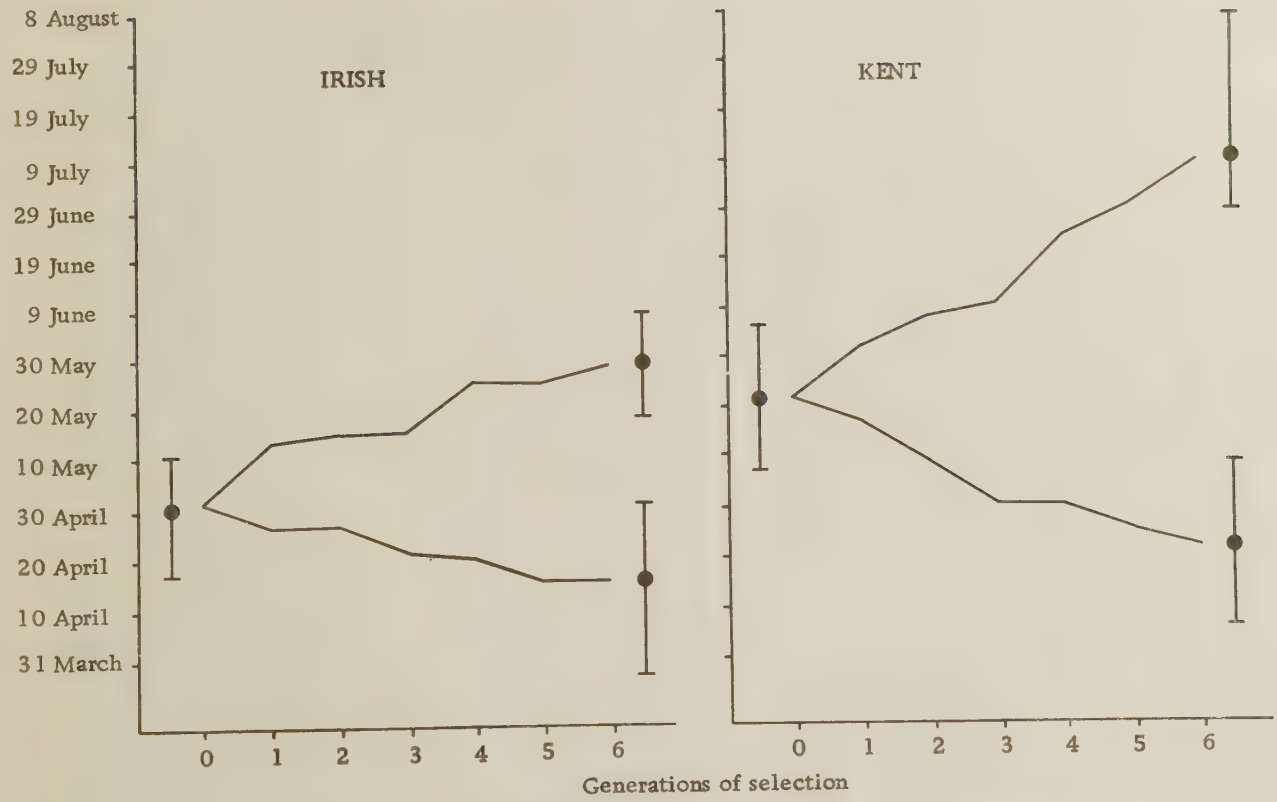


Fig.1. Response to selection for date of ear emergence in Irish and Kent perennial ryegrass (Lolium perenne) (from Cooper 1961)

This rapid response to selection for heading date was associated with correlated changes in certain other characters. No effects on leaf and tiller development in the vegetative stage could be detected, but the early-flowering selection lines tended to have smaller ears and fewer spikelets. The most marked correlated changes were in seed and pollen fertility which were appreciably reduced, particularly in the late-flowering selection lines. These changes which were often associated with cytological abnormalities, may in part have been a result of inbreeding during the selection programme, although the vegetative vigour of the plant showed no deleterious effects of inbreeding.

These combined physiological and genetic studies on flowering responses which determine two important agronomic features of the ryegrass crop, persistency and maturity date, revealed the wealth of genetic variation carried within these cross-fertilizing grass varieties for these particular characteristics and their rapid response to selection. These results therefore suggested that other important physiological characters of the grass plant might show similar genetic control, and be equally susceptible to change under selection (5).

Studies on the physiologic and genetic basis of other important agronomic characteristics including flowering responses in other grass species, the seasonal pattern of leaf and tiller development and the uptake of and response to soil nutrients were therefore started. At the same time the potentialities of this combined physiological and genetic approach to the improvement of production characters led to the setting up in 1959-60 of the Department of Developmental Genetics equipped with the appropriate laboratory and growth room facilities for physiological and biochemical work.

3. Flowering responses in other forage grasses

The elucidation of the sequence of flowering responses in Lolium led to a survey of these responses in other species, followed by more critical studies in Dactylis, Phleum and Phalaris (6, 1). Most annual temperate grasses, like the spring cereals and Westernwolths and Wimmera ryegrass, possessed little or no requirement for cold or short day induction, and were usually long-day in their photoperiodic response. The comparatively simple sequence of responses found in Lolium, however, did not necessarily apply to other perennials. In the first place, many perennial species, such as Avena elatior, Dactylis glomerata, Festuca pratensis and Poa pratensis, although they apparently need to be exposed to winter conditions in the field, cannot be induced to flower by either cold or short-day treatments given to the imbibed seed or young seedling. Many varieties of Dactylis, for instance, appear to possess a juvenile stage during which the seedling is unable to respond to either cold or short-day. Secondly, the inductive requirements, once the juvenile stage is past, do not necessarily involve exposure to both cold and short photoperiod. Lolium perenne can respond to either cold or short-day, but Bromus racemosus can be induced by cold but not by short-day, while the species of Agrostis tested required short-day but not cold. Thirdly, both Phleum and Arrhenatherum, although perennial, have no inductive requirement for cold, but ear initiation is inhibited by high temperatures in the summer.

In the temperate grasses therefore, the perennial habit is based on the maintenance of an adequate number of vegetative shoots in the late summer and early autumn, but this end-result can be achieved by several different developmental responses. In each of the species studied more intensively, however, the quantitative responses of different varieties were closely related to their past selection history. In Phalaris tuberosa, for instance, which is of Mediterranean origin, the flowering responses of locally adapted populations are closely related to the length of the possible growing season as limited by the onset of summer drought.

4. Leaf expansion in climatic races

The ability to expand leaf surface actively through the year, particularly during the low temperatures and low light intensities of winter, is an important breeding objective. In view of the current interest in the potential winter production of Mediterranean collections of forage grasses, a survey was made of leaf growth and cold hardiness in contrasting climatic populations of Lolium perenne, Festuca arundinacea and Dactylis glomerata from continental, maritime and Mediterranean origins, using the controlled environments available in the Department of Agricultural Botany. The optimum temperature for leaf extension growth and rate of leaf appearance was about 20°C for all populations. At 30°C, leaf growth per tiller was reduced, largely through a decrease in leaf size, but with little difference between the relative performance of the different climatic races. At sub-optimal temperatures, however, at 10°C and even more so at 5°C. regular differences appeared between the contrasting populations of each species. The Mediterranean material could expand leaf surface quite actively at 5°C, while the continental populations became semi-dormant with very little leaf expansion; the maritime populations were intermediate in response (5). The relative performance of these varieties at moderately low temperatures (5°C) in the controlled environments was closely correlated with their leaf expansion when grown outdoors in December, but unfortunately proved to be inversely related to their cold hardiness as measured in a standard freezing test.

A similar range of variation in leaf expansion at moderately low temperatures was revealed between contrasting populations of Phalaris tuberosa from the Mediterranean region in studies carried out (by JPC) in the Ceres Phytotron at Canberra in 1962; here again the rate of leaf expansion at low temperature (5°C) was inversely related to the mean temperature of the coldest month in the place of origin.

This association between active leaf growth at moderately low temperatures and susceptibility to frost damage is unfortunate from the breeding point of view, and it is important to discover how far these two characteristics are inevitably associated physiologically or how far they have simply been selected together in the original habitat. A possible physiological basis of this association was studied by Eagles (11) using two contrasting populations of Dactylis glomerata, one from Portugal and the other from Norway (Fig.2), and two of Lolium perenne, one from Lithuania and one from Algeria. Only slight differences were found in the assimilation rates of the northern and Mediterranean varieties at low temperatures (5°C) but a marked difference in the use of the

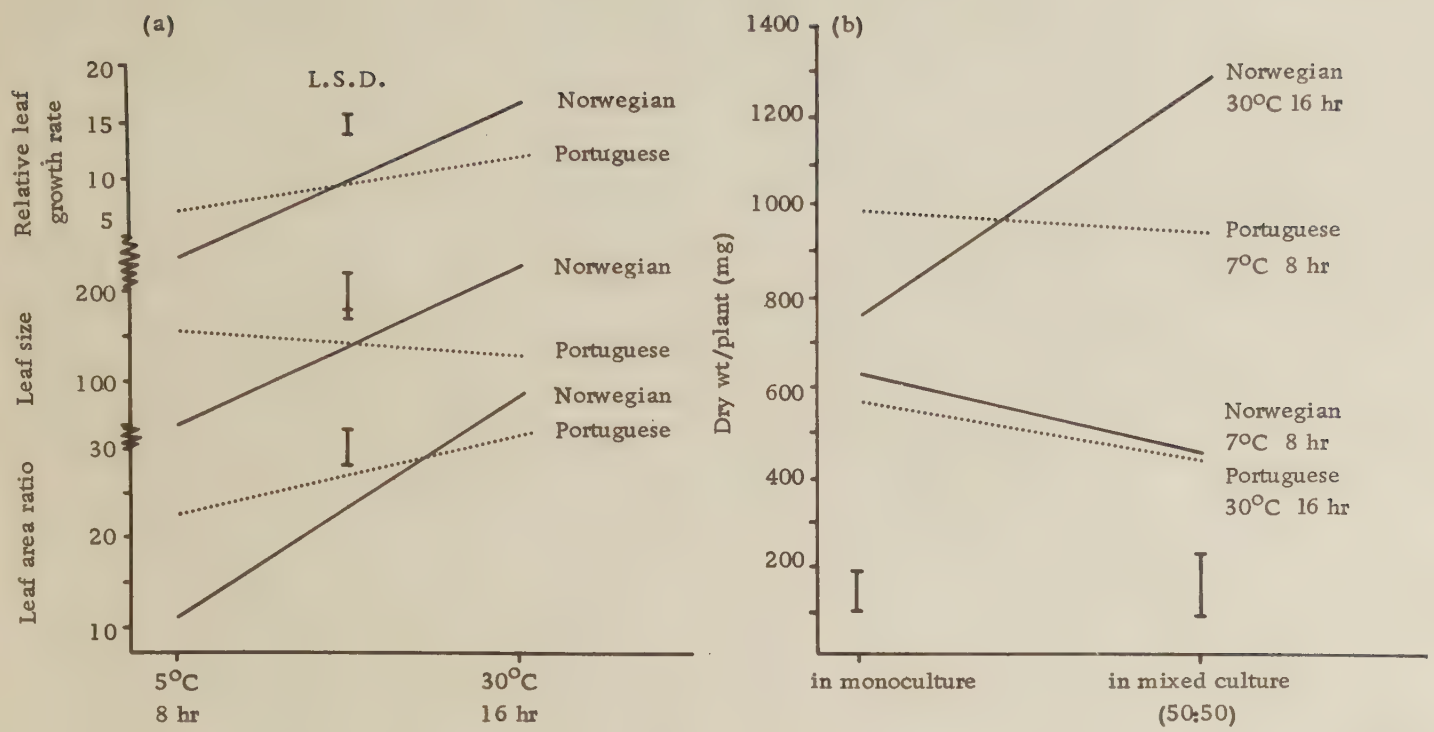


Fig.2. Leaf growth and competitive ability in a Portuguese and a Norwegian population of cocksfoot (Dactylis glomerata) in contrasting environments

assimilates by the plant. In the Mediterranean populations the assimilates were used actively for new leaf growth, with little accumulation at the base of the shoot. In the northern populations, however, there was little or no extension growth and the assimilates accumulated in the leaf bases usually in the form of fructosans, with associated winter hardiness.

5. Genetic control of leaf growth

The high heritability and rapid response to selection for flowering date in ryegrass led to the examination of genetic variation in leaf growth and its components, leaf size and rate of leaf appearance, in both Italian and perennial ryegrass varieties (14). Both leaf size and rate of leaf appearance showed reasonably high heritabilities and responded rapidly to selection; after four generations of selection, leaf size in the large lines was more than twice that in the small lines. These two components of leaf growth, however, proved to be inversely correlated; selection for large leaves resulting in slower leaf appearance, and selection for more rapid leaf appearance in smaller leaves. There was thus no regular effect of such selection on dry matter production in the seedling stage, similar production being obtained from plants with a large number of small leaves or with a smaller number of large leaves. Later studies by Wonkyi-Appiah also showed that such selection had no regular effect on photosynthetic rate of the individual leaves or on dry matter production under sward conditions.

The developmental basis of these differences in leaf size or in rate of leaf appearance was examined by Edwards (13) who found that selection had little influence on the rate of leaf initiation on the shoot apex, or on the rate of elongation of the developing leaf. It had, however. markedly affected the duration of elongation of the individual leaf, i.e. the interval between initiation and complete expansion. Selection for a shorter interval between the appearance of successive leaves thus reduced the time available for elongation growth and hence led to shorter leaves. Encouragingly high heritabilities for these two components were also obtained by R.L.Thomas. using a diallel analysis between 6 contrasting populations. although leaf size showed marked maternal effects in the young seedling stage.

6. Variation in response to soil nutrients

A survey of variation in response to soil nutrients, particularly nitrogen, and in resistance to aluminium and manganese toxicity, which can be important in acid soils, was begun by P.B.Vose (19). He found marked variation between ryegrass varieties in resistance to both manganese and aluminium, but was able to select more resistant lines from within susceptible varieties. Resistance was often related to the cation exchange capacity of the material. As part of this programme he also developed techniques for sand and water culture, and used these to screen individual genotypes of ryegrass for high and low response to nitrogen (20). This work was later continued by Holmes, who examined the heritability of nitrogen response and obtained small, though encouraging, values.

7. Nutritive characteristics

In view of the current interest in the nutritive value of herbage, pilot investigations were also made in collaboration with the Chemistry Department into the variation and heritability of such components as in vitro digestibility, soluble carbohydrate content and crude protein content. This work indicated the existence of variation between genotypes for many of these nutritive characters, and selection lines for such characters are now being actively developed by the Herbage Breeding Department.

The pilot investigations listed above suggested that a wealth of genetic variation was available in the forage grasses for a wide range of physiological and biochemical characters which influence the seasonal production of the crop and its nutritive value to the animal. Furthermore, estimates of heritability indicated that many of these characters could be manipulated in a breeding programme by the usual genetic techniques of selection, although unfavourable correlated responses might well occur (5, 7).

DEVELOPMENT OF CURRENT APPROACH (1964-69)

The next step was to examine the relevance of these findings in terms of improving the production of the grass crop in the field and particularly in terms of setting up selection programmes for those characteristics which limit such production. This stage of the research programme was associated with the development of laboratory and controlled environment facilities in the new Stapledon Building which was opened in 1964. With the background information on the physiology and genetics of production characters already acquired, it was possible to develop the current approach of attempting to identify those physiological and biochemical features of the grass plant which determine its production under sward conditions and to assess the amount of genetic variation available for these characteristics and its potential manipulation in a breeding programme (7, 9).

The grass crop is grown as a source of digestible energy and other nutrients, including protein and minerals, for the ruminant. The energy is derived from the seasonal input of solar radiation and the soil nutrients from the particular fertilizer regime employed. The ultimate limit to production is thus set by the seasonal input of solar energy, but the use of this energy by the plant can be limited by two other important climatic factors, low temperature and water stress, or by a shortage of soil nutrients, particularly nitrogen. The plant breeder is thus basically concerned with the efficiency of the crop in converting these inputs of energy and nutrients into a form most suitable for the animal, and with the possibility of improving it by selection and breeding. As a first step in this approach, it was therefore decided to examine the efficiency of energy conversion by existing varieties of forage grasses at three levels of increasing complexity:- (i) the individual leaf or young seedling, when fully exposed to light, (ii) the crop canopy, when intercepting all the incoming light energy, and (iii) the established sward, grown without limitations of water or nitrogen and harvested to maintain adequate light interception through the year (9).

At the same time, the appointment of P.J.Goodman in 1965 gave an opportunity to intensify the search for variation in response to soil nutrients, particularly to the major elements, nitrogen, phosphorus and potassium, while the appointment of K.J. Treharne in 1966 made it possible to investigate the biochemical basis of variation in energy and nutrient conversion, particularly the activity of possible rate-limiting enzyme systems concerned with photosynthesis and with nitrogen and phosphorus metabolism. Subsequently, the award of two Nuffield Fellowships in Applied Plant Physiology made it possible to attract two physicists into the research programme, one, J.M. de Jager, to develop infra-red gas analysis equipment for measuring photosynthesis and transpiration of the individual leaf, and the other, J.E.Sheehy, to develop instrumentation for measuring incoming radiation and its distribution through the canopy.

1. Photosynthetic activity of the individual leaf or young seedling

(i) Growth analysis

Growth analysis techniques were used to examine the seasonal changes in relative growth rate, net assimilation rate and leaf area ratio in seedlings of Mediterranean, maritime and continental varieties of Lolium, Festuca and Dactylis (16). The seasonal pattern for these components was similar to that reported for other species, relative growth rates reaching a maximum of 0.15-0.17 g/g/day in July to August and declining to very low levels in mid-winter. Net assimilation rate followed closely the seasonal input of light energy, varying from below 1.5 g/m^2/day in mid-winter to about 8-9 g/m^2/day in the summer. Leaf area ratio, on the other hand, showed the highest values (25-35 mm^2/mg) during late autumn and declined to below 20 mm^2/mg in March and April. The conversion of light energy by this young seedling material varied from over 15% during the low light intensities and moderate temperatures of early winter, down to 2-3% at high light intensities in the summer. The differences in winter production between the Mediterranean and continental populations of these grasses proved to be based on variation in leaf area ratio (i.e. in distribution of assimilates) rather than in net assimilation rate.

A subsequent survey of four ryegrass varieties using growth analysis in controlled environments clarified the response of this material to changes both in temperature and light intensity. Net assimilation rate increased rapidly at low light intensities, but reached maximum values at about 30,000 lux. Leaf area ratio, on the other hand, decreased from the lower light inputs, so that relative growth rate reached a plateau at about 20,000 lux. The temperature optima for net assimilation rate and for relative growth rate were about 20°C, but leaf area ratio showed little change over the range 5°-30°C. As in the earlier outdoor studies, about 15% conversion of light energy was achieved at low light intensities (1500 lux) but only 3-4% at intensities over 20,000 lux. A given input of light energy, however, was converted more effectively when supplied at a constant intensity during 16 hours in the growth room, than when provided as a normally fluctuating daily input outdoors. Consequently, the net assimilation rates and relative growth rates obtained at 20°C 16 hour photoperiod, and 20,000 lux in the growth rooms were some 10% higher than those recorded outdoors in July.

In a further comparison of a wider range of varieties of Italian and perennial ryegrass at low and high light intensities, Wilson and Cooper (21) found significant varietal differences in all growth analysis components. At both intensities, the varietal differences in relative growth rate within the Italian and within the perennial group were based on differences in net assimilation rate rather than in leaf area ratio, but the Italian group had greater leaf area ratios than the perennial at each light intensity.

Controlled environment facilities were also used by Tainton to examine the light and temperature requirements for vegetative growth of a range of tropical grasses including Paspalum dilatatum, Hyperrhenia hirta and Eragrostis curvula. These tropical species proved to have much higher optimum temperatures for net assimilation rate and relative growth rate (over 30°C), compared with about 20°C for the temperate perennial ryegrass. Furthermore, while perennial ryegrass reached light saturation at about 20,000 lux, the assimilation of the tropical Paspalum dilatatum increased up to the highest light intensity used of 80,000 lux (8).

Such growth analysis techniques can evidently be used to examine the general effects of the light and temperature environment on growth and assimilation. However, since they are based on serial destructive harvesting, their degree of precision is low, nor can they be used to separate the effects of previous and current environmental conditions. More precise methods for measuring the instantaneous photosynthetic rate of individual seedlings or individual leaves were therefore required.

(ii) Infra-red gas analysis

With the aid of a grant from the Nuffield Foundation a multi-channel infra-red gas analysis circuit was constructed by de Jager to provide precise measurements of instantaneous rates of photosynthesis and transpiration. This equipment can measure the photosynthetic rate of ten individual grass leaves at a time under controlled temperatures, light intensities and CO_2 concentrations. Associated psychrometric equipment is used to measure transpiration rates and hence leaf resistances, while the construction of soil moisture probes makes it possible to study the effect of soil moisture on photosynthetic rate and transpiration. This equipment is now being used to examine the response of photosynthesis to light and temperature in species and varieties of forage grasses, and the effect of previous environmental conditions on the photosynthetic activity of the leaf. It also serves as a standard for calibrating the Warburg and C^{14} techniques which are being used to measure photosynthetic rates in individual leaf pieces.

Pilot studies have shown that for such temperate species as Lolium perenne, Dactylis glomerata and Festuca arundinacea, light saturation occurs at about 20,000 lux with a maximum photosynthetic rate of 20 to 25 mg of $CO_2/dm^2/hr$, in contrast to such tropical species as Paspalum dilatatum which can make use of much higher light intensities and can reach a maximum photosynthetic rate of over 60 mg $CO_2/dm^2/hr$. All the temperate species examined have rather broad temperature optima around 20°C, but the optima for the tropical species are much higher, usually over 30°C, and at

15°C, even at high light intensity, their photosynthetic rate is lower than that of the temperate material. In the temperate grasses, these photosynthetic rates correspond to about 15% conversion of light energy at low light intensities, decreasing to less than 2% conversion at light saturation (9).

Similar infra-red gas analysis equipment has been used by Eagles in a study of the effects of previous and current light and temperature conditions on the assimilation and growth of two contrasting climatic populations of Dactylis glomerata, one from Portugal, the other from Norway (12, 18). There were significant correlations between the different measures of photosynthetic activity employed, i.e. net assimilation rate (growth analysis), net photosynthetic rate (infra-red gas analysis), $^{14}CO_2$ incorporation into leaves, and the activity of carboxydismutase(RUDPCase)in cell free preparations. Photosynthesis increased with current light intensity in both populations, but the potential rate of the Portuguese variety was greatly increased when the plants were grown at high light intensity, while that of the Norwegian variety remained unchanged. The Norwegian population, however, had a much greater photosynthetic rate, transpiration rate and carboxydismutase activity than the Portuguese when both were grown at 5°C or 15°C, but there were no differences between the populations when grown at 25°C (Fig.3) (12, 18).

(iii) Warburg equipment

The infra-red gas analysis equipment allows of the precise measurement of photosynthesis and transpiration on the attached leaf under controlled conditions of light intensity, temperature and CO_2 concentration, but for rapid screening purposes a more rapid technique, which can handle large amounts of material, is desirable. For this purpose, a modified Warburg technique has been developed for measuring the photosynthetic rate of small leaf pieces of grasses and cereals under controlled light and temperature conditions (Plate 1). The results of this technique compare well with those from infra-red gas analysis, and it can be used to examine leaves taken from any experimental conditions in the field, glasshouse or growth room.

This technique has been used by Wilson to examine the photosynthetic response to light intensity and CO_2 concentration of varieties of perennial ryegrass from contrasting climatic or agronomic origins. He found significant differences between populations and between individual genotypes both in the maximum photosynthetic rate at light saturation, and in the photosynthetic rate when light was limiting. The differences in maximum photosynthesis were negatively correlated with mesophyll cell size, possibly because of cell volume to surface area relationships in the mesophyll, but there were no obvious morphological differences associated with variation in light-limited photosynthesis. The effect on photosynthetic rate of the conditions under which the individual leaves developed was also examined. Either high light intensity or low temperature during the development of the leaf markedly increased its potential maximum photosynthesis, but this effect did not operate through changes in mesophyll cell size or number. Following this discovery of variation in photosynthetic rate, Wilson assessed its heritability using a diallel cross between six contrasting genotypes

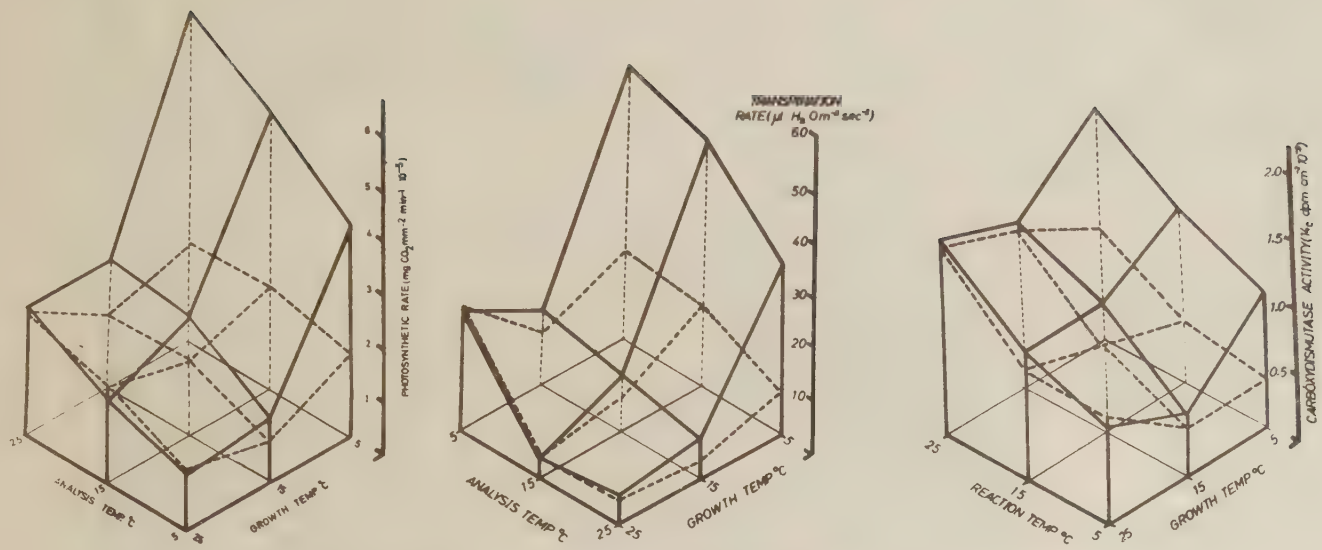


Fig.3. Effect of temperature on photosynthesis, transpiration and carboxydismutase activity in a Portuguese and a Norwegian population of cocksfoot (Dactylis glomerata) (from Treharne and Eagles 1970).

Plate 1. Warburg technique for measuring photosynthetic activity of individual grass leaves.

of perennial ryegrass, and found encouragingly high values (over 60%) for light-saturated photosynthesis, and about 30% for light-limited photosynthesis, indicating the possibility of useful response to selection. He also found that selection within a single variety for small mesophyll cell size produced a marked increase in photosynthetic rate and net assimilation rate in the progeny, though this was balanced by a decrease in leaf area ratio (10).

This technique is now being used to compare a wider range of populations of both perennial and Italian ryegrass, to select for high and low maximum photosynthesis within individual ryegrass varieties, and to trace seasonal changes in photosynthetic capacity in grass varieties in the field.

All these techniques for measuring photosynthetic activity indicate that in the temperate grasses, the individual leaf or young seedling shows the usual type of photosynthetic response to light intensity with light saturation at 20,000 to 30,000 lux, and a maximum photosynthetic rate of 20-25 mg $CO_2/dm^2/hr$, corresponding to about 2% conversion of light energy. For tropical grasses, the light saturation level is much higher with correspondingly greater maximum photosynthesis (over 60 mg $CO_2/dm^2/hr$). The optimum temperature for photosynthesis in most temperate grasses is around 20°C, but is much higher, over 30°, for tropical species; in fact, at temperatures of below 15°C the maximum photosynthetic rates of temperate grasses are greater than those of tropical. Appreciable variation occurs both within and between species in the maximum photosynthetic rate and in the response of photosynthesis to temperature, providing opportunities for further selection.

(iv) Biochemical aspects of photosynthesis

The detection of such genetic variation in both light-limited and light-saturated photosynthesis led to comparative biochemical studies on the activity of possible rate-limiting enzyme systems concerned with photosynthesis, including the carboxylating enzymes (RUDPCase in temperate grasses, PEPCase in tropical grasses), the Hill reaction and photophosphorylation.

Appropriate techniques for the analysis of these systems in forage grasses have been developed by Treharne, and variation in their activity has been detected within and between grass species (Fig.4a). In a range of ryegrass varieties differences in carboxydismutase activity were correlated with maximum photosynthetic rate, while in climatic populations of Dactylis, the temperature and light induced changes in photosynthetic rate were closely associated with changes in carboxylating activity but showed little correlation with the Hill reaction or photophosphorylation (18, 12).

The temperature sensitivity of the contrasting carboxylating enzymes in tropical and temperate grasses also differs. The optimum temperatures of the RUDPCase operating in the temperate Avena and Lolium proved to be around 20°C, while that of the PEPase in the tropical maize and Cenchrus was over 30°C. Further comparative studies by Miss Julie Pughe on a range of crop species have shown a close correspondence between the temperature response curves for photosynthetic rate, as measured by

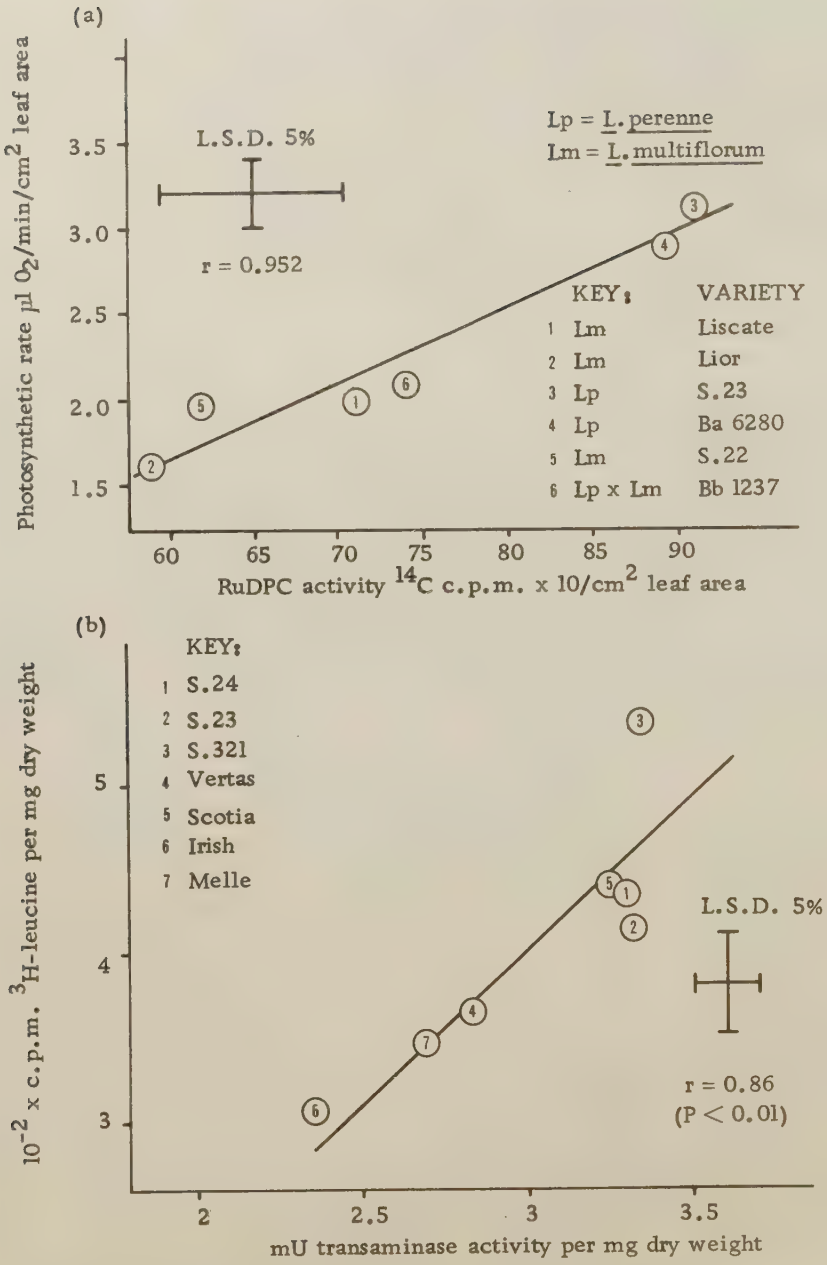


Fig. 4. (a) Variation in photosynthetic rate and carboxydismutase activity in varieties of Lolium multiflorum and L. perenne.

(b) Variation in protein synthesis and transaminase activity in varieties of L. perenne.

a C^{14} dip technique, and those of the appropriate carboxylating enzyme.

More fundamental studies by Treharne and Stoddart on the possible control of carboxylating activity by such growth regulators as gibberellins and cytokinins have shown that photosynthetic rate can be markedly influenced by the level of endogenous and applied growth regulators, and that these changes are parallelled by the activity of the carboxylation step which may be rate-limiting, even under field conditions.

2. Light interception by the canopy

Although variation in the photosynthetic rate of the individual leaf is an important component of energy conversion, in practice the grass crop is grown as a closed canopy, in which the incoming light is reflected or transmitted to varying depths depending on the arrangement of the leaves in the canopy. With a prostrate growth habit and fairly horizontal leaves, most of the light will be intercepted near the top of the canopy, but with more erect leaves the light will penetrate to a greater depth and be spread over a greater leaf area index, with correspondingly greater efficiency of conversion.

Pilot studies on the relationship between crop growth rate, leaf area index and light profile down the canopy in erect (S.22) and prostrate (S.23) ryegrass varieties showed marked differences in the extinction coefficient between the erect and prostrate forms, and corresponding differences in the optimum leaf area index and the maximum crop growth rate. At a low leaf area index, the prostrate leaves intercepted more light and hence gave a greater crop growth rate, but at a higher leaf area index, the erect growth habit resulted in the greatest crop growth rate. Estimates of crop growth rates from such canopies at complete light interception gave values of up to 20 g/m^2/day in the middle of summer, corresponding to 5-6% conversion of light energy, appreciably higher than that of the individual leaves. At low light intensities in early winter, however, crop growth rates of less than 3 g/m^2/day were obtained giving conversion figures of 12-15%, similar to those of the individual leaf (9).

These studies on variation in light interception and its effect on energy conversion and dry matter conversion have been continued by Ian Rhodes, using varieties of ryegrass of contrasting growth habits. Using a stratified clip technique, he confirmed the marked difference in light profile, in critical leaf area index, and in maximum crop growth rate between erect and prostrate varieties, and showed that these differences in canopy structure resulted in a marked interaction between cutting frequency and dry matter production; the prostrate varieties gave relatively higher yields than the erect forms under more frequent cutting, and vice versa. Furthermore, certain mixtures of erect and prostrate ryegrass varieties (e.g. Ba 6280 and S.23) appeared to give more efficient light interception down the profile and a higher crop growth rate than the pure varieties (17). Rhodes then selected individual genotypes with contrasting leaf lengths and habits of growth from within a single ryegrass variety, and found that canopies of these contrasting genotypes showed similar differential effects of leaf arrangement on dry matter production. Certain mixtures of two contrasting genotypes proved more efficient than either of the component types; on the other hand, all mixtures

of three or more genotypes gave yields intermediate between the highest and lowest yielding components (Fig.5). It is evidently possible to select both within and between varieties for more efficient leaf arrangement, in relation to particular systems of cutting.

With the aid of a grant from the Nuffield Foundation, Sheehy has been studying the physical aspects of light penetration. He has constructed tube solarimeters with appropriate filters and used these to measure the extinction coefficient for both visible and infra-red radiation in contrasting grass canopies (Plate 2), and then using a stratified clip technique has been able to relate these to differences in the optimum leaf area index and the maximum crop growth rates. The 'k' values varied from 0.7-0.8 in the prostrate varieties, to 0.2-0.3 in the more erect forms, with corresponding differences in the critical leaf area index. In the same experiments he also measured the photosynthetic response to light intensity of the individual leaves in the canopy, and found that in his material, the range in crop growth rate between varieties from 23 to 42 g/m^2/day in early June was based on differences in light interception, rather than in photosynthetic rates of the individual leaves.

It is clear, therefore, that in a vegetative canopy at complete light interception, the leaf arrangement can have a marked effect on the penetration of light down the canopy, the critical leaf area index and the potential crop growth rate. The optimum leaf arrangement and habit of growth will depend on the height and frequency of harvesting but, clearly, useful genetic variation exists for these characters and can be used in a selection programme.

3. Biological potential of an established sward

From a knowledge of the pattern of light interception down the canopy and of the photosynthetic response of individual leaves to both light and temperature, estimates can be obtained of the potential photosynthesis of a grass canopy through the year, assuming that water and nutrients are not limiting and that the crop is maintained at optimum light interception throughout. In practice, however, the grass crop is subjected to a series of harvests, either by cutting or grazing, and it is important to check any estimate of potential photosynthesis against the actual production attainable in an established sward harvested regularly through the year.

A simulated sward technique has therefore been developed, in which varieties and selection lines are grown in small plots outdoors, without limitations of water or soil nutrients, and under a system of harvesting which maintains adequate light interception but minimizes senescence and decay at the base of the sward. This technique involves 6-7 cuts through the year, from early March to the end of October, with a nutrient input of up to 600 kg/ha nitrogen and corresponding amounts of phosphorus and potassium. Using this system of management, highly-tillering varieties of perennial ryegrass, such as S.23, have revealed a potential of well over 20,000 kg dry matter/ha/annum, including over 2,500 kg/ha of crude protein. The highest annual production recorded was over 29,000 kg/ha from the recently developed ryegrass variety, Ba 6280,

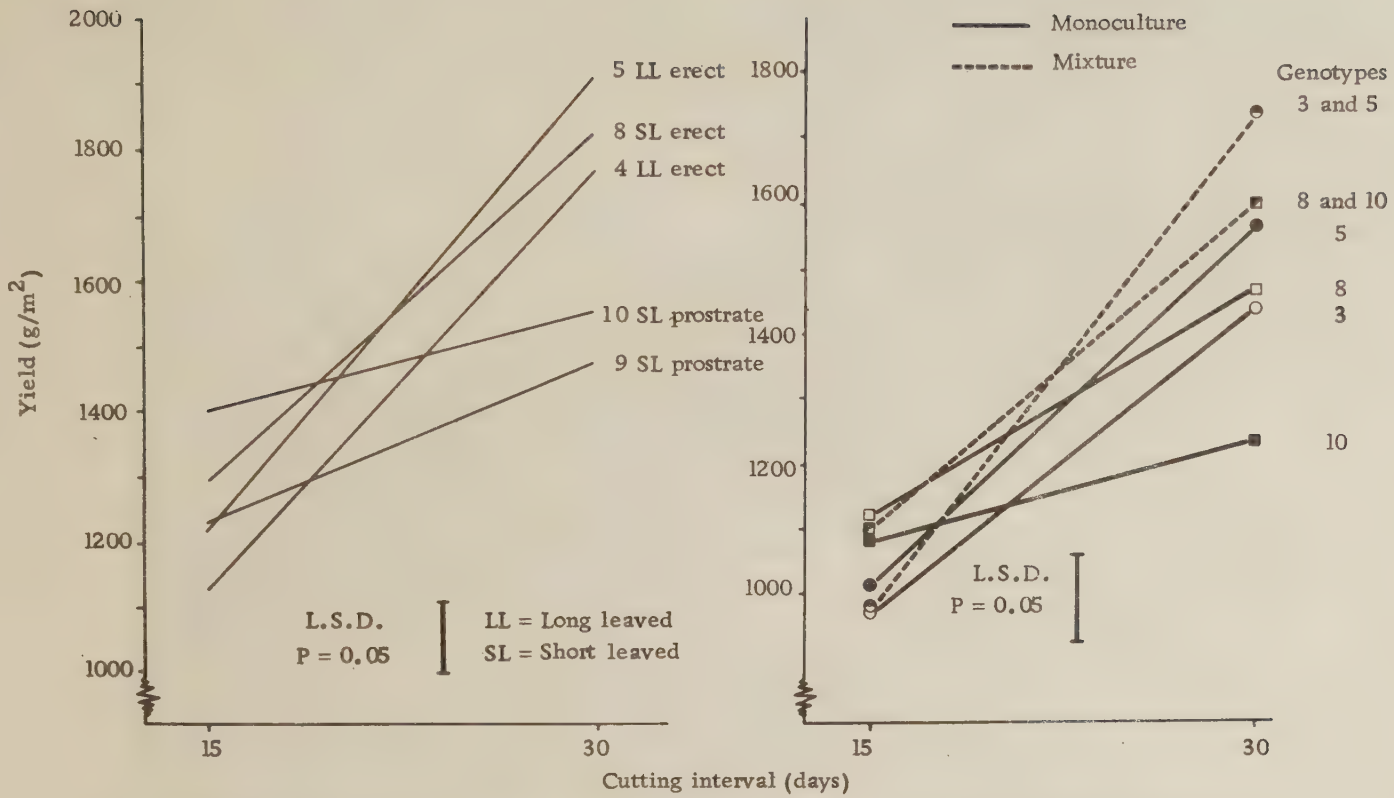


Fig.5. Effect of selection for leaf form on (a) dry matter production and on (b) ecological combining ability in a single variety of perennial ryegrass (Lolium perenne).

Plate 2. Use of tube solarimeters to measure light interception in grass canopies .

corresponding to 3-4% conversion of the incoming light energy through the year.

During the summer period, April-September, conversion figures of 4-5% were obtained, but during October-March, only about 2.5% of the low intensity light energy was fixed, probably due to low temperature limitations. The crop growth rates achieved ranged from 140-170 kg/ha/day in the summer period (April-September) to less than 20 kg/ha/day for October-March. With this frequency of cutting, the digestibility (DOMD) was maintained above 66% and the crude protein content above 12%. Under this management, involving cutting at 5-7 week intervals, Italian ryegrass and the less persistent Irish perennial give appreciably lower yields than the more highly tillering persistent varieties, such as S.23 and Ba 6280. Under a conservation management, however, higher dry matter yields might well be obtained from Italian ryegrass (9).

These high potential yields and the marked differences between varieties are, however, only revealed at high fertilizer inputs, where light and temperature are the only limiting factors. At nitrogen levels below 200 kg/ha, few varietal differences could be detected.

Such dry matter yields are much greater than the average production from grassland in Britain which is probably 6-7000 kg/ha of dry matter, but this is based on an average nitrogen input of only 50-60 kg/ha. Dry matter yields of up to 15,000 kg/ha are already being achieved by a number of intensive grassland farmers using high fertilizer inputs and high stocking rates.

In terms of both digestible energy and protein, these potential yields from the grass crop compare favourably with those from other farm crops. For example, under British conditions, a good cereal crop with a grain yield of 5,000 kg/ha (about 40 cwt/acre) achieves only 0.5% conversion of the annual input of light energy, and a protein yield below 600 kg/ha, largely because the crop occupies the land for only a portion of the year (most of the dry matter in the grain being derived from photosynthesis during only a few weeks before and after anthesis), and also because the economic yield includes only part of the total dry matter. A potato crop of 50,000 kg/ha (about 20 tons/acre), which maintains an active leaf canopy for most of the summer, can convert rather more light energy, over 1%, although here again only part of the total dry matter is used.

Although the energy and protein yield from grass is considerably higher than from other field crops, it requires serial harvesting either by grazing or regular cutting, consists of fresh material with a high water content which is difficult to conserve, store and transport, and of course must be processed through the animal. Even so, as an energy source for the ruminant, the biological margin between grass and a cereal crop is considerable.

4. Response to soil nutrients

In practice, the input of fertilizers, particularly of nitrogen, is often the factor limit-

ing grassland production, but although the fertilizer levels can be controlled by the farmer, it is important to develop varieties which use soil nutrients efficiently both in terms of dry matter production and in terms of mineral content in relation to animal requirements. The earlier studies by Vose and Holmes had indicated differences between grass varieties in their response to and uptake of nitrogen and various cations, including potassium, calcium and magnesium.

Following these results, extensive screening tests have been set up to examine differences in the response of both cultivated varieties and natural populations of ryegrass from different soil types to the major soil nutrients. Significant differences in response to nitrogen, phosphorus and potassium have been obtained (Fig. 6a), not necessarily correlated with total dry matter production, and selection lines both for efficient response and for high content have been established (15). Pilot studies by Miss Anne Bowerman on the biochemical basis of nitrogen metabolism in terms of nitrate reductase activity (Fig. 6b) and other enzyme systems concerned with protein synthesis, such as transaminase (Fig. 4b), have also revealed variation between genotypes for these possible rate-limiting processes. Similar biochemical variation in the rate of photophosphorylation, and in the early products of phosphorylation, such as sugar-phosphate and nucleotides have been found by C.K. Shurety between genotypes of perennial and Italian ryegrass. A pronounced "carry-over" effect of phosphorus nutrition on seedling performance has also been detected in ryegrass and in barley, influencing both the germination and growth of the seedling, and the products of phosphorylation.

It is evidently possible to select for more efficient response to particular nutrients or for a higher content of them. The particular responses needed in practice will depend on the cost and availability of fertilizers and also on the use to be made of the grass crop in the farming system: whether it is to be regarded primarily as an energy source, to be supplemented with protein and minerals from elsewhere, or whether a complete and balanced diet is required.

FUTURE DEVELOPMENTS

The present investigations have revealed the high potential production of many current ryegrass varieties, when grown without limitations of water and soil nutrients, and when managed to provide adequate light interception through the year; an annual potential of well over 20,000 kg/ha, corresponding to over 3% conversion of the incoming light energy is not uncommon. The biological potential of other grass and legume species and the effect of contrasting harvesting systems, including conservation treatments, are now being examined. Techniques have also been developed to examine such important components of production in the sward as the pattern of light interception by the canopy, the photosynthetic activity of the individual leaves, and the distribution of assimilates in relation to regrowth after defoliation.

We now need to know which of these components and their associated physiological and biochemical characteristics are most important in limiting production under sward conditions.

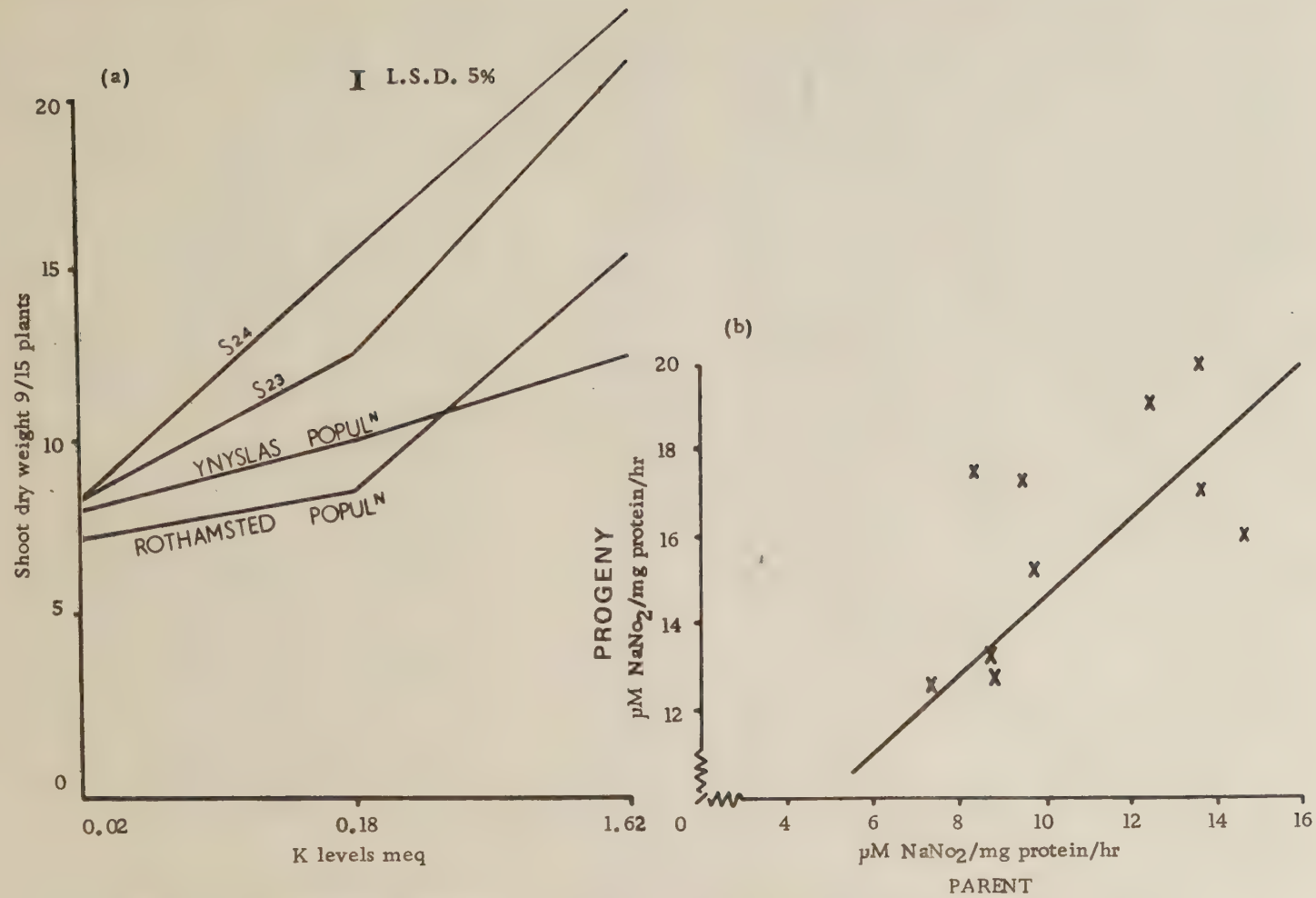


Fig. 6. (a) Response to potassium in populations of perennial ryegrass (Lolium perenne).
(b) Heritability of nitrate reductase activity in populations of perennial ryegrass (L. perenne).

Future improvement of energy and nutrient conversion by the grass crop may well involve such physiological features as a high light saturation level and associated maximum photosynthetic rate, together with more effective light distribution down the crop, to make better use of the high light intensities of summer; and also more active photosynthesis and/or leaf expansion during the low light intensities and low temperatures of late autumn and early spring. In addition, adaptation to particular systems of harvesting, such as rotational grazing or conservation managements will be important, as will efficient response to, and uptake of soil nutrients, with particular reference to the nutritional requirements of the ruminant.

Genetic variation is known to exist for many of these physiological or morphological characteristics, and appropriate selection programmes have been established.

The current research programme is providing a knowledge of the biological potential of grass species and varieties, and also an understanding of the physiological and biochemical features of the crop which may limit the conversion of energy and nutrients. It is also establishing appropriate screening techniques and demonstrating the existence of useful genetic variation for many of these characteristics. The next important step is to use this genetic variation to build up new and improved varieties, specifically tailored to particular environmental inputs and particular systems of management.

During the next few years, therefore, it should be possible to see how far a knowledge of the physiological and genetic basis of these production processes can be used to synthesize varieties with improved energy and nutrient output under sward conditions in the field.

References

(1) D.M.Calder, 1965, Proc.12th Easter Sch.Agric.Sci.Univ.Nott. 59-73.
(2) J.P.Cooper, 1951, J.Ecol. 39, 228-70.
(3) J.P.Cooper, 1954, J.Ecol. 42, 522-56.
(4) J.P.Cooper, 1961, Heredity, Lond. 16, 435-53.
(5) J.P.Cooper, 1963, Environmental Control of Plant Growth. Academic Press, 381-403.
(6) J.P.Cooper and D.M.Calder, 1964, J.Br.Grassld Soc. 19, 6-14.
(7) J.P.Cooper, 1965, Proc.12th Easter Sch.Agric.Sci.Univ.Nott. 293-307.
(8) J.P.Cooper and N.M.Tainton, 1968, Herb.Abstr. 38, 167-76.
(9) J.P.Cooper, 1969, Occ.Symp.No.5, Br.Grassld Soc. 5-13.
(10) J.P.Cooper and D.Wilson, 1970, Proc.XI Int.Grassld Congr. 522-527.
(11) C.F.Eagles, 1967, Ann.Bot.N.S. 31, 31-9.
(12) C.F.Eagles and K.J.Treharne, 1969, Photosynthetica 3, 29-38.
(13) K.J.R.Edwards, 1967, Genet.Res. 9, 247-57.
(14) K.J.R.Edwards and J.P.Cooper, 1963, Heredity, Lond. 18, 307-17.
(15) P.J.Goodman, 1969, Symp.Br.Ecol.Soc.No.9, 237-53.
(16) D.MacColl and J.P.Cooper, 1967, J.appl.Ecol. 4, 113-27.

(17) I. Rhodes, 1969, J. Br. Grassld Soc. 24, 123-7.
(18) K. J. Treharne and C. F. Eagles, 1970, Photosynthetica 4 (2), 107-117.
(19) P. B. Vose, 1963, Herb. Abstr. 33, 1-13.
(20) P. B. Vose and E. L. Breese, 1964, Ann. Bot. N. S. 28, 251-70.
(21) D. Wilson and J. P. Cooper, 1969, Ann. Bot. N. S. 33, 951-65.

PLANT PATHOLOGY

A.J.H.CARR

Right from the early beginnings of the Station, it was appreciated that disease was likely to be a major problem hindering the plant breeder in his efforts towards crop improvement. At that time the diseases of herbage had not been studied exhaustively and, although those that beset cereals were rather better known, there was still scope and need for further study. It was to be almost 40 years before a Plant Pathology Department could be established, but the foundations were laid by the detailed and meticulous investigations of Miss Kathleen Sampson, then Senior Lecturer in Agricultural Botany at the University College of Wales, and Dr.J.H.Western who, in 1937, with the aid of a research grant provided by the Ministry of Agriculture, carried out a survey of the diseases affecting herbage plants throughout Britain, which formed the basis of what still remains the standard British reference work on this subject (14). Valuable assistance and advice was also rendered to the Stations' breeders in those early days by D.Walters Davies and J.R.W.Jenkins, Advisory Mycologist and Advisory Entomologist respectively, to the U.C.W.Agriculture Department.

It was considered from the outset that the main function of the Plant Pathology Department, set up in 1958, should be to provide a service to the plant breeder by investigating the relative importance of the various diseases, devising infection techniques and assessing disease reaction in a wide range of genetic material. Clearly, this has involved, and will continue to involve, the closest collaboration with the breeder at all stages of the breeding programme, and also with other disciplines such as physiology and biochemistry. Nor have the fundamental biological and epidemiological aspects been ignored, for it is only by a complete understanding of the whole of the disease cycle that practical methods of tackling these problems are likely to present themselves. Work on cereal and forage crop pathogens is being undertaken.

The dynamics of herbage diseases are often as complex as the crop itself - a crop whose value is not intrinsic but is measured in terms of animal products. Hence assessment of disease impact must take into account not only the effect on total yield but on nutritive quality as well. In this context, the discovery that many common fungal pathogens reduce potential leaf carbohydrate by as much as 50% is of major significance (3). In the field of grassland pathology one is concerned more with the effect of disease on the total ecology of the sward than on individual spaced plants. The work of P.L.Catherall on this subject has established that the importance of herbage viruses can be estimated accurately only in terms of their effect on the competitive ability of infected plants in the sward, which in turn is related to their influence on

growth habit (6). These discoveries have led to the tentative suggestion that it may well prove more efficaceous to breed for ultra-susceptibility to some of these viruses than for a type of resistance short of immunity.

Up to 1952 the graminaceous viruses had received only scant attention; indeed, only cocksfoot streak had been reported in Britain. At the present time some 15 viruses have been identified, several of them as a result of work at Aberystwyth (4). Few are restricted to either grass or cereals; most are capable of infecting both, the perennial grasses providing a permanent reservoir of virus for periodic infection of the annual cereal crop via the appropriate insect vectors. A feature of this grass reservoir is that it may harbour certain virus strains so lethal to cereals as to be virtually self-eliminating were it not for their maintenance in the perennial host (5). Programmes to incorporate barley yellow dwarf virus resistance into barley, in collaboration with the breeders concerned, are already well advanced (7), and more recently sources of resistance to oat mosaic virus have been isolated (10). It is, however, necessary to increase our understanding of the epidemiology of these viruses, particularly those factors which influence the movement of their insect vectors within and between grass and cereal crops, and to find more critical ways of assessing the level of virus infection in breeders' material. In the account which follows J.A'Brook reviews problems and progress in this field.

CURRENT RESEARCH INVESTIGATIONS

1. Oat mildew

In recent years plant breeders have been turning their attention increasingly towards the prospect of utilizing "field" or "horizontal" resistance to many pathogens. This type of resistance is not absolute and is often expressed more in the adult plant than at the seedling stage, but present evidence suggests that, being polygenically rather than single-gene controlled, it is less race-specific and therefore less likely to be eroded by the evolution of new pathogen races. It is important to understand host/pathogen interactions at the cell level which determine this type of resistance, and to examine whether these are different from mechanisms governing race-specific resistance. A detailed account of work along these lines will be published elsewhere, but a brief review of current findings by A.J.H.Carr is given here. Complementary work in this field is reported in the account of Arable Crop Breeding.

The work was carried out on four lines of oats, one highly susceptible (C.I.4877), one susceptible (var. Milford), one moderately field resistant (var. Maldwyn) and one, an Avena byzantina line, with an extremely high level of field resistance (Cc 4761). Plants were grown to the fifth leaf stage and segments from all leaves were inoculated on benzimidazole solution with a single, virulent mildew race by I.T.Jones (Arable Crop Breeding). These were then fixed in acetic alcohol 2, 5 and 10 days after inoculation, stained in cotton blue/lactophénol and examined under the light microscope. Mycelium was clearly visible on the leaves of susceptible oats within 2 days of inoculation. Sporulation had begun after 5 days and was abundant after 10 days. There

was little obvious difference either in lesion density or in sporulation between the first and last-formed leaf. With Maldwyn, by contrast, surface mycelium became increasingly more sparse and attenuated on successively developed leaves, while with the highly field resistant A. byzantina (Cc 4761) few spores appeared to develop beyond the appressorial stage on any but the first-formed leaf. On both these populations sporulation was delayed considerably and greatly reduced.

Counts were made of the number of successful spore penetrations, i.e. those that resulted in development of haustoria. Only 28% of spores which germinated on the first-formed leaf of the A. byzantina population had succeeded in penetrating the host after 2 days incubation, and this value fell sharply to less than one per cent on the 4th and 5th leaves. Although with a 5-day incubation period penetration on the first leaf had risen to 97%, none of the succeeding leaves had levels in excess of 15%. However, peak spore penetration of the remaining three lines occurred not on the first but on the third-formed leaf, with much higher values after only two days incubation of 72% on C.I. 4877, 52% on Maldwyn and 29% on Milford. The position of the moderately field resistant variety Maldwyn is an interesting one, for although the amount of surface mycelium undoubtedly reduced on successively formed leaves this was not paralleled by a reduction in successful spore penetrations until the 4th and 5th leaves, when the values fell sharply below those recorded for the more susceptible variety Milford.

Critical examination showed that, with the A. byzantina line, the infection peg apparently had considerable mechanical difficulty in penetrating the host cuticle and epidermal cell wall. although in some instances a definite host reaction could also be seen. With this line, and to a lesser extent with Maldwyn, even successful penetration frequently resulted in small haustoria with few and stumpy digitate processes. Presumably these would be far less efficient in function than normal haustoria which generally follow penetration of fully susceptible hosts.

It would appear from these observations that field resistance in the oat populations investigated depended partly on a failure of many germinating spores to penetrate the host tissues and partly on the development of a greater proportion of structurally less efficient haustoria leading to sparser aerial growth and a reduction in sporulation. The field resistance of the A. byzantina line seemed to depend more on the former and that of Maldwyn more on the latter. Both these mechanisms contrast with the post-penetration type of resistance based on hypersensitivity of the host-cell which is often associated with race-specific resistance.

2. Verticillium wilt of lucerne

Previous work by A.J.H. Carr has established that the lucerne strain of V. alboatrum produces toxin-like substances in liquid culture capable of simulating many features of the wilt syndrome (12). The chemical composition of these has been largely determined (16). Whether this very simple and rapid technique has application to resistance breeding depends clearly on whether toxin tolerance is heritable and under the control of the same genetic system as that which determines the degree of fungus-induced

wilting.

Three lucerne populations, which form an integral part of the breeding programme and are therefore known to differ in resistance to wilt, were selected for further investigation: the susceptible variety Du Puits, the progeny originating from a cross between Du Puits and Medicago gaetula having moderate resistance, and progeny derived from a cross of Du Puits with a natural M. sativa x M. falcata hybrid having a high degree of resistance. Seedlings of each population were placed in culture filtrate and, on the basis of their wilt reaction, 5 relatively toxin-tolerant and 5 toxin-susceptible were selected from each population and raised to maturity. A more critical assessment of all 30 plants was then made by recording the mean wilting (scale 0-4) of 10 cut shoots of each plant placed in culture filtrate. A chain cross was made within each group of 5 plants and 20 seedling progeny from each family were tested for wilting in culture filtrate. The mean scores given in the table show the effects of selection within each population for high and low toxin reaction. Not only were the parent and progeny values consistently higher in lines selected for toxin susceptibility, but the overall reactions reflected the natural level of resistance to the pathogen in each population. A correlation coefficient of 0.51 (P = 0.01) was obtained between the 30 parent and progeny means, indicating that, like natural resistance, toxin tolerance was heritable. From this and earlier work it may be concluded that similar, if not identical, genetic mechanisms control resistance both to V. alboatrum and to the wilt-toxins that this pathogen produces. It not only indicates the possibility of utilizing the technique in resistance breeding, but also provides indirect evidence of the intrinsic role played by toxins in the etiology of this vascular wilt; were this not so, it seems unlikely that host response both to the pathogen and its metabolic products would be under the control of virtually the same genetic system.

Population	Parents selected from:	Mean parent value	Mean progeny value
Du Puits	Toxin tolerance	1.17	1.98
	Toxin susceptibility	1.48	2.38
Du Puits x M. gaetula	Toxin tolerance	0.64	1.56
	Toxin susceptibility	0.82	1.69
Du Puits x (M. sativa x M. falcata hybrid)	Toxin tolerance	0.32	1.23
	Toxin susceptibility	0.58	1.86

3. Oat sterile dwarf virus

In a previous report (17) reference was made to the possibility of oat sterile dwarf virus (OSDV) being present in a crop of Mostyn oats grown at the Station which also contained European wheat striate mosaic virus (EWSMV). Further work by Catherall has established that this was so. Of 254 nymphs and adults of the planthopper Javesella

pellucida Fabr. caught in or near the infected crop during August and September and transferred singly to healthy Mostyn oat seedlings, 16% transmitted OSDV only, 9% EWSMV only and 5% transmitted both viruses. This is the first record of OSDV in Britain, although the virus is known in Eastern Europe and Scandinavia.

Infected plants were severely stunted, deep blue-green in colour and produced a profusion of juvenile shoots having 2-3 much shortened, misshapen leaves. Panicle emergence was completely, or almost completely, suppressed. Conspicuous enations developed on veins on the abaxial leaf surfaces of oat plants inoculated in the glasshouse, but were absent from plants infected naturally in the field. The virus was transmitted by J. pellucida to wheat, oats, barley, meadow fescue, Italian and perennial ryegrasses. Natural infection of ryegrasses in the spaced-plant nursery has been noted in successive seasons since 1967. Like infected oats, these are extremely dwarfed, blue-green in colour and rarely survive for more than a few months.

4. Oat mosaic virus

A previous report (18) described the discovery of this soil-borne virus in the winter oat nursery at the Station and gave some account of the main properties. In addition to natural soil transmission, the virus could also be transferred from and to oats, the only known host, by sap-inoculation, but with only 5-20% success. P.L.Catherall has since found that the addition of celite abrasive or a phosphate buffer to the inoculum did not increase the transmission rate. However, when the inoculum was sprayed on the leaves from a laboratory spray-gun operating at 70 p.s.i., the rate of success was increased to 40-50%. The time taken for the first signs of infection to appear varied considerably with the method of infection. Autumn-sown oat plants in the infected field did not develop symptoms until spring, whereas plants in pots of infected soil showed symptoms in 3-5 months if overwintered in a sheltered position, but not at all if kept in a heated glasshouse. By contrast, manual inoculation resulted in symptoms within 15-20 days, but unless the plants were maintained under cool conditions these were usually transient and were rarely as severe as in plants infected naturally.

5. Lolium mottle virus

A previously unidentified virus has been isolated by J.A'Brook from plants of perennial ryegrass and crested dogstail (Cynosurus cristatus) sent by Dr. C. O'Rourke, Agricultural Institute, Carlow, Eire, and designated Lolium mottle virus (LMV). Symptoms in the original hosts consisted of a faint chlorotic mottle, especially on the younger leaves. The virus has been sap-inoculated into S.22 Italian ryegrass, S.24 perennial ryegrass, S.50 timothy and crested dogstail. In all cases symptom expression was poor. Neither symptoms nor recovery of virus were achieved from manually inoculated S.59 red fescue and S.170 tall fescue. LMV was readily sap-inoculable to, and recoverable from, a wide range of cereals, including varieties of spring and winter oats, barley, wheat and rye. Symptoms in cereals varied from pronounced mottling to general chlorosis and even necrosis of leaves, together with dwarfing.

Preparations from grass hosts proved difficult to achieve owing to low concentrations of the virus, but those from Jufy wheat showed under the electron microscope numerous polyhedral particles ca 30 nm diameter. These were identical with paritcles seen in leaf-dip preparations from the original hosts. Preparations also contained smaller (16-20 nm diameter) polyhedral particles, suggesting the presence of a satellite virus.

6. Epidemiology of cocksfoot mottle and Phleum mottle virus

Both these viruses are transmitted by the beetles Lema melanopa and L. lichenis, have different grass hosts but some cereal hosts in common and can be manually inoculated in similar fashion (15, 8). In addition to the reported host-range, Phleum mottle virus (PMV) has recently been inoculated successfully to Bromus sterilis and also to a number of barley varieties, from which it can be purified more readily.

Epidemiological work by D.A.Benigno and J.A'Brook has paid particular attention to the problem of why cocksfoot mottle virus (CFMV) infected cereals readily when inoculated by vector or sap, yet does not occur naturally in the crop. In general all cereals tested tended to be more susceptible at growth stages 1 and 2 (N.A.A.S.scale), and to become less so at later stages of their growth. Comparisons of feeding habits made by measuring the area of leaf eaten in a given time and by observing activity at intervals revealed that, contrary to field observations, these vectors preferred grasses to cereals. While L. melanopa showed a greater preference for cocksfoot than for timothy, the reverse was true for L. lichenis. Within cereals, L. melanopa preferred wheat to barley and oats, whereas L. lichenis preferred barley to wheat or oats. L. melanopa oviposited most frequently on oats, followed in order of preference by cocksfoot, timothy, barley and wheat. The site most favoured by this species was the upper leaf surface, whereas L. lichenis preferred the tiller bases.

Adult L. melanopa acquired CFMV readily from cocksfoot and wheat and transmitted the virus to both these hosts but not to oats or barley. Transmission only to cocksfoot occurred with oats as the virus source. The table shows the efficiency of various methods of CFMV and PMV transmission from healthy to infected plants.

Virus	Manual inoculation	Crushed together	Cut together	Cut sequentially	Vector transmission: L. melanopa	L. lichenis
CFMV	75	60	26	11	30	10
PMV	53	28	22	19	20	10

These findings confirm earlier evidence (13) that, in the grass crop, mechanical methods are of greater importance than vector transmission in the spread of these viruses. Lack of natural infection of the cereal crop appears to be due to age of the crop at the time of beetle migration following winter hibernation precluding easy infection.

In the course of the work an apparent tolerance to CFMV has been discovered in

some lines of wild and cultivated cocksfoot. The nature and possible use of this tolerance in a resistance breeding programme is being investigated.

7. Epidemiology of ryegrass mosaic virus

Extensive surveys by J. A'Brook in southern England made in cooperation with the Grassland Research Institute and N.A.A.S. on ryegrass seed crops from 1967-69 have shown a higher incidence of ryegrass mosaic virus (RMV) in S.22 Italian than in S.321 perennial ryegrass. In each year, spring-sown crops of both varieties under barley had a higher incidence of the virus the following spring than crops sown direct in the autumn. In a cooperative trial at the G.R.I., winter kill in perennial ryegrass swards following a mild autumn was most marked in plots receiving a high level of nitrogen coupled with infrequent defoliation. Plant loss appeared to be associated with the incidence of RMV in these plots. The results throw some light on one possible cause of degeneration in swards of this species.

8. Virus diseases of agricultural Brassicae

Although there is considerable information on the distribution and effects of viruses in horticultural brassica crops, rather less is known regarding the agricultural species, particularly rapes and kales. Experiments have therefore been initiated by S.A.Shoyinka and A.J.H.Carr to determine virus incidence and the extent of host variation available for possible resistance-breeding programmes in these crops.

Brevicoryne brassicae and Myzus persicae, the main aphid vectors of the two most important brassica viruses, cabbage black ringspot and cauliflower mosaic, reach their peak numbers in July/August, by which time the crops are already past their most susceptible growth-stage, while during the flight season the proportion of these two species is low relative to total aphid numbers. These factors, together with the virtual absence of other types of brassica crops capable of providing continuity of virus source throughout the season, may account for the failure to isolate these viruses in a survey of some 30 crops of rape, kale, swede and turnip in the Aberystwyth area. However, the situation may be very different in other areas where agricultural and horticultural brassica crops with overlapping growth seasons are cultivated.

Varietal assessment of rapes, kales, swedes and turnips against several isolates of cauliflower mosaic, cabbage black ringspot, turnip yellow mosaic and turnip crinkle viruses in the open, the glasshouse, and in controlled environments under different light and temperature regimes showed yield losses ranging from one to 98 per cent. There was as much within as between variety variation (Plate 1), but although some degree of host genotype/virus isolate interaction was evident, in general a somewhat similar pattern of host response resulted from infection with all 4 viruses, indicating that selection for resistance to one might well confer similar levels of resistance to the other viruses. These preliminary results indicate that, although a considerable degree of phenotypic stability in agronomic type has been achieved within these essentially outbreeding crops, there is adequate variation in resistance and tolerance to virus infection within existing varieties to enable some improvement to be accomplished, pro-

Plate 1. Four turnip varieties, three plants of each, showing variation in reaction to cauliflower mosaic virus, both within and between varieties.

vided that the variation noted is heritable. Although radish has proved both more difficult to infect and more tolerant of infection than other host species, practical difficulties of hybridization would severely limit its usefulness as a general source of resistance.

9. Behaviour of aphid vectors

Trapping of aphids has been carried out by J. A'Brook using vertical cylindrical and horizontal flat sticky traps, 1 m and 0.3 m above ground level, respectively. Eighteen different paint finishes (including "fluorescent") covering the range from red to blue, together with black and white, were used with each type of trap to determine the colour sensitivity of each aphid species as well as to provide information on species incidence and differences in patterns of behaviour.

On the assumption that horizontal traps catch only those aphids about to land, while vertical traps catch mainly flying aphids by impaction together with some landing at low wind speeds, it would be expected that the numbers of aphids caught on the two types of traps should bear the same relationships over the range of colours used. While this was true for Aphis fabae, Rhopalosiphum padi (both sexes), R. oxyacanthae (males) and Macrosiphum (Sitobion) avenae, it was not so for Cavariella aegopodii, Capitophorus hippophaes, Rhopalosiphum insertum (females), Metopolophium dirhodum, Cryptomyzus carduinus, Anoecia corni or Elatobium abietinum. Macrosiphum euphorbiae showed an intermediate response, similar relationships between the two types of trap obtaining over the range of normal paint finishes but not with fluorescent, whereas the converse was true for Hyperomyzus lactucae. These differences between trap catches could not be ascribed to colour response alone, since assuming a preference for yellow over white only certain species (A. fabae, R. padi males and females, R. oxycanthae males, M. euphorbiae, M. dirhodum, C. carduinus, M. (S.) avenae and H. lactucae) were colour sensitive while others (C. aegopodii, R. oxycanthae females, A. corni and E. abietinum) were not.

Since it is possible that the original assumption of the respective functions of the two types of trap was not wholly valid, a means of measuring the "landing component" caught on vertical sticky traps was devised, in which the normal cylindrical traps were compared with similar ones having a horizontal cap, and with horizontal traps having the same surface area set up level with the top and bottom of cylindrical traps. Theoretically, the catch on the normal cylindrical trap should have equalled that on the capped cylindrical trap plus a "landing component" on the horizontal traps. For all species, the cap reduced the numbers of aphids caught to less than half that of the normal trap, indicating the size of the actively landing component. Myzus (Nectero-siphon) persicae and R. padi females came closest to fulfilling theoretical expectations. Restuls with other aphid species (R. padi males, R. oxyacanthae females, C. hippophaes, Ceruaphis eriophori and Pemphigus spp.) also fulfilled the expected relationship provided that a larger horizontal component than strictly theoretical was assumed. An interesting feature both of this and the trial using different trap colours was the different behavioural patterns often shown by males and females of the same

species.

Trials were conducted in 1969 to determine whether spacing of grass affected aphid populations in a similar way as has been demonstrated in other crops (1). Previous evidence from virus incidence in the grass crop had suggested that this might be so. In one trial, drills of cocksfoot were sown at 0.15 m and 0.53 m spacings, together with further 0.53 m spaced drills having red clover between, and red clover alone. For comparison purposes a second trial utilized drills of 3 kale varieties at 0.30 m and 0.90 m spacings. Cylindrical traps at 1 m and horizontal traps at 0.3 m were set up in both, painted jasmine yellow (B.S. 0.001) in the cocksfoot and lime green (B.S. 0.008) in the kale. Greater numbers of Hyalopterus pruni, M. dirhodum and R. oxyacanthae were caught on vertical traps over the 0.53 m spaced cocksfoot drills than over any other plot, but catches of A. fabae, Fordiniae spp. (mainly F. geoica), M. euphorbiae, M. (S.) avenae, M. persicae, and R. padi did not vary significantly between types of plot. A significantly greater number of aphids of the species M. dirhodum, R. oxyacanthae females and R. padi females were caught on horizontal traps (i.e. in the landing phase) over 0.53 m spaced than over 0.15 m spaced cocksfoot drills, although this was not so for R. padi males or for A. fabae. The numbers of aphids caught in the remaining two types of plot did not differ significantly from the 0.15 m cocksfoot drill spacings. Further, the order of difference between catches at 0.3 m and 1 m trap heights was the same over all drill spacings, indicating that both traps were measuring the same effect, i.e. landing on the traps.

In the kale trial A. fabae, C. hippophaes, Pemphigus spp., R. maidis, R. oxyacanthae and R. padi were caught more frequently over wide than over close spaced kale on vertical traps. The response at 0.3 m above ground by "landing" aphids was shown only by R. padi but, as in the cocksfoot trial, differences between plots were of the same order at both trap heights. Two species, A. fabae and R. padi females, shown earlier to be particularly sensitive to yellow, were caught on vertical traps in greater numbers over early purple broccoli than over the light green kales.

These studies on aphid incidence have been continued in 1969 using a "40 ft" Rothamsted pattern trap and a Johnson 12 in suction trap at 1 m. The catches have been identified in situ and weekly summaries of the collaborative survey have been published by Rothamsted Experimental Station.

OPERATIONAL PROJECTS

A very recent development is the establishment of a Screening Unit under the immediate direction of the Department but in close liaison with the plant breeders. This fulfils a need to translate the research information into operational programmes, and although functional only since 1968, the Unit has already made a substantial contribution.

1. Crown rust of ryegrass

A simple glasshouse technique for screening bulk populations of ryegrass for resist-

ance to Puccinia coronata var. lolii has been developed and used by P.W.Wilkins. This consists of distributing dry uredospores in talc by means of a cyclone sprayer attached to a standard aerosol laboratory spray gun over plants at the 4-5 tiller stage maintained at relatively low humidity. Following inoculation, the humidity is raised by means of rotary humidifiers and maintained at saturation point for 48 hr. Provided night temperatures below 15°C can be maintained, symptoms appear some 10-16 days later and plants are then scored for infection and ranked on a scale based on the density of lesions and the degree of sporulation. Recently it has been found possible to store collections of uredospores without marked loss of viability by ampoule freeze drying, provided that they are allowed to absorb atmospheric moisture for 24 hr prior to inoculation.

Using this technique, selections have been made within the Station-bred varieties S.23, S.24 and S.101 perennial ryegrass and S.22 Italian ryegrass. All of these varieties have been found to contain a reasonable proportion of highly resistant, though not immune, genotypes. Although the full results of progeny testing from crosses of resistant plants within these varieties are not yet complete, it seems likely that this resistance is of the stable, broad spectrum "field" or polygenic type.

An interesting development of the programme arises from the finding that amphiploids derived from crosses of S.22 Italian ryegrass with S.170 tall fescue, developed by Elfed Lewis (Herbage Breeding), are immune to this rust, presumably deriving their immunity from the tall fescue parent. However, there is some preliminary evidence that the precise inheritance of this immunity is likely to be complex. Second generation progeny derived from backcrosses of this hybrid material with the Italian ryegrass parent contained a higher proportion of near-immune genotypes than expected on a simple Mendelian basis, while only 4% were markedly susceptible compared with 60% of the recurrent parent line. The position with P. coronata var. festucae, which attacks Festuca but not Lolium spp., with regard to these amphiploids is being investigated.

Preliminary work with systemic fungicides applied as foliar sprays at varying concentrations has been undertaken to determine whether this might offer a method of quantifying crown rust resistance levels in more precise terms. Of the range tested, Plantvax gave remarkable control of crown rust in glasshouse experiments, the degree of control being determined both by concentration and by the genetic level of resistance in selected perennial ryegrass clones. Thus, a highly susceptible clone gave a fully susceptible reaction (score 9) at a concentration of 0.11 g/litre and a moderately resistant reaction (score 3) at 1.76 g/litre, whereas the corresponding values for a resistant clone were 4 and 1.5 (highly resistant) respectively. Differences between clones and fungicide levels over the whole experiment, comprising 12 genotypes and 3 concentrations, were highly significant ($P = 0.01$).

2. Stripe rust of cocksfoot

Techniques similar to those described for crown rust have been used by P.W.Wilkins

to screen Station-bred varieties of cocksfoot for resistance to Puccinia striiformis. Considerable genotypic variation in stripe rust reaction has been found within S.143 and S.345, and a selection and hybridization programme is in progress. Collaborative investigations with Miss D.Schmidt, a visiting worker from the Swiss Federal Research Station, Nyon, have established a relationship between leaf carbohydrate, winter dormancy and stripe rust susceptibility. The biochemical aspects of these findings are at present under investigation in collaboration with K. J. Treharne (Developmental Genetics). In the meantime, care is being taken to avoid sources which depend for their "resistance" on undesirable biochemical characters such as low carbohydrate levels.

3. Drechslera leafspots of grasses

The development by P.W.Wilkins of a technique for large-scale conidial production in Drechslera (syn. Helminthosporium pro parte) spp. has allowed him to begin a programme of resistance screening against these important grass pathogens. Mature colonies of the fungi on potato-dextrose agar are leached in running water for 48 hr, after which abundant conidia are produced within 2 weeks. This simple technique has yielded spore densities at least equal to those obtained by more elaborate methods of stimulation involving critical control of spectral energy, temperature and nutritional requirements (Plate 2). An aqueous suspension of the spores is sprayed on the test plants and the level of infection is scored after 2 weeks. D.siccans requires a continuous level of very high humidity to be maintained in the glasshouse throughout the incubation period; satisfactory results can be obtained with D.dictyoides with only intermittent periods of high atmospheric moisture.

As a preliminary to more extensive breeding investigations an attempt has been made to characterize the reactions of a range of ryegrasses, fescues and their hybrids to these two common Drechslera spp. D. siccans attacks ryegrasses more readily than fescues, and no useful sources of resistance have been isolated within the restricted range of Italian or perennial ryegrass varieties tested thus far. However, as for crown rust, amphiploids between S.22 Italian ryegrass and S.170 tall fescue showed a significant degree of resistance, presumably derived from the tall fescue parent. By contrast with D.siccans, D.dictyoides attacks fescues rather than ryegrasses. Like Braverman and Graham (2) we find two forms of this species among our isolates: a coarse-stranded, protothecial type (f.sp. dictyoides) and a fine-stranded type lacking protothecia in culture (f.sp.perenne). On the rather narrow range of host material tested, f.sp.perenne infected S.215 meadow fescue but not S.170 tall fescue, while f.sp.dictyoides infected S.170 but not S.215. The amphiploids were virtually immune to both formae speciales of D.dictyoides, presumably deriving their immunity in this instance from the Italian ryegrass parent. Thus there seems to be a distinct possibility of utilizing these amphiploids to derive resistance to the two common Drechslera spp.infecting the Lolium/Festuca complex.

4. Cereal viruses

The Screening Unit has recently assumed responsibility through P.W.Simmonds for

Plate 2. Conidial production by Drechslera siccans on agar plates two weeks after aqueous leaching.

collaboration in the operational aspects of the programme of breeding for resistance to these viruses. Following P.L.Catherall's discovery (11, 9) that specific genes from Ethiopian sources conditioning tolerance to barley yellow dwarf virus tend to lose their effectiveness when introduced into the slower growing European barleys, an attempt is being made to broaden the base of the work by investigating the type of genetic background which will allow these tolerance genes full expression. Varieties having a short growing season are being examined from this point of view.

One of the major problems with oat mosaic virus is the development of a technique which will allow more rapid testing of potential parental material and of segregates than is possible in the field. An attmept is being made to improve the efficiency of sap-inoculation and to determine whether the response of a wide range of genetic material to sap and soil-borne infection is identical.

FUTURE DEVELOPMENTS

The research to date clearly indicates that, with respect to disease, herbage and cereal crops cannot be regarded as separate entities. The techniques which have been, and are being developed must be utilized towards a clearer understanding of the epidemiological factors which relate the two types of crop. Sampling methods to assess virus vector incidence and behaviour need to be extended to permit accurate estimation of the proportion of an insect population carrying virus within and between crops at a given time. Although it is commonly assumed that within the Gramineae fungal pathogens have a more restricted host-range, specific evidence of this is often lacking. Intensification of disease incidence following increasing cultivation of cereals in areas where grassland formerly predominated suggests the possibility of a direct, as well as an environmental, relationship similar to that demonstrated for the viruses; the one crop providing a perennial source for infection of the other. This problem is worthy of investigation. Solution of these epidemiological problems would enable more effective use of control methods to be made - methods which require, for their development, an integrated approach by the plant pathologist, plant breeder, biochemist and chemist.

If, as seems certain for the reasons stated earlier, greater reliance in future is placed on "field" or "non-race-specific" resistance in the production of new crop varieties, an integrated approach assumes even greater importance. This type of resistance and its handling is reasonably well-known in out-breeding crops, but application to the inbreeding cereals will require the development of new techniques. The plant pathologist has an important contribution to offer here, particularly in determining the morphological and physiological interaction of host and pathogen genetic systems at all levels, including that of the host cell. The mechanisms which govern host response to any particular virus or virus strain seem even less well understood, and require elucidation both in genetic and physical terms, if progress is to be made in resistance-breeding.

Although both quantitative and qualitative losses in herbage yield due to disease

have been demonstrated to be of greater significance than is often realized, the precise magnitude of this loss will depend, among other factors, on the type of management practised. It is certain to be greatest when the crop is harvested at a mature stage of growth and in seed production. The Screening Unit has demonstrated the feasibility of selection for enhanced resistance to several pathogens from within indigenous varieties and will undoubtedly assume an increasingly important role in the work of the Department.

References

(1) J.A'Brook, 1968, Ann.appl.Biol. 61, 289-294.

(2) S.W.Braverman and J.H.Graham, 1960, Phytopathology 50, 691-695.

(3) A.J.H.Carr and P. L. Catherall, 1964, Report of the Welsh Plant Breeding Station for 1963, 94-100.

(4) A.J.H.Carr, 1968, Span 11, 92-95.

(5) P.L.Catherall, 1963, Pl.Path. 12, 157-160.

(6) P.L.Catherall, 1966, J.Br.Grassld Soc. 21, 116-122.

(7) P.L.Catherall and J.D.Hayes, 1966, Euphytica 15, 39-51.

(8) P.L.Catherall, 1970, Pl.Path. 19, 75-78.

(9) P.L.Catherall, A.T.Jones and J.D.Hayes, 1970, Ann. appl. Biol. 65, 153-161.

(10) P.L.Catherall and J.D.Hayes, 1970, Pl.Path. 19, 78-81.

(11) A.T.Jones and P.L.Catherall, 1970, Ann.appl.Biol. 65, 137-145; 147-152.

(12) S.H.Michail and A.J.H.Carr, 1966, Trans.Br.mycol.Soc. 49, 133-138.

(13) 1968 Rothamsted Expl Stn Report for 1967, 126.

(14) Kathleen Sampson and J.H.Western, 1954, Diseases of British Grasses and Herbage Legumes, 2nd ed., C.U.P., 118 pp.

(15) E.P.Serjeant, 1967, Ann.appl.Biol. 59, 31-38.

(16) J.L.Stoddart and A.J.H.Carr, 1966, Ann.appl.Biol. 58, 81-92.

(17) 1968 Welsh Pl.Breed.Stn Report for 1967, 119.

(18) 1968 Welsh Pl.Breed.Stn Report for 1967, 118.

CHEMISTRY

D.I.H.JONES

Chemical evaluation has played an important role in the breeding and investigational work of the Station from the outset, although a Chemistry Section was not established until 1953. Prior to this, the Agricultural Chemistry Department of the U.C.W. collaborated closely with the Station, beginning with the researches of Stapledon and Fagan in the 1920s.

This early work was aimed at investigating the extent of species and varietal variation in certain chemical constituents with emphasis on the comparison of commercial and indigenous varieties (5). Such comparisons clearly indicated the important differences in composition between the leaf and stem fractions of grass and the way in which composition would be modified by the selection of leafy varieties. This knowledge undoubtedly influenced the breeding of the first S varieties, characterized by their leafy growth compared with their commercial counterparts.

Although applied to a wide range of grasses, the scope of the evaluation carried out by Fagan and his colleagues was necessarily limited by the techniques then available. It is interesting, in retrospect, to note that the significance of several of their results has only been fully appreciated in the last decade. The high fibre content of cocksfoot as compared with ryegrass and other grasses, for example, was clearly shown, and the need to study digestibility appreciated. It was only in the 1950s, however, that the digestibility of pure species and varieties was studied, and the low digestibility of cocksfoot shown. Fagan and his colleagues also recognized that digestibility differences would be less marked and not as important in regrowth, as compared with primary growth, since new growth was being dealt with. They concluded that to assess the intrinsic value of individual grasses it was necessary to recognize yield, persistency, composition and digestibility.

Fagan also studied the effects of nitrogen fertilizer on chemical composition, showing for example, how nitrogen content could be increased by fertilizers, the effect being more marked in the leaf than in the stem. An interesting observation was that the stem of some grasses was better grazed than that of others, and Fagan concluded that the palatability of stems appeared to be largely governed by their fibre content. This conclusion is particularly apposite to our current thoughts regarding the reasons for differences between grasses in voluntary intake by grazing animals.

Another important aspect of the work concerned hill land investigations. These

showed the limitations to plant growth impaired by the poor nutrient status of upland soils and also the poor quality of upland herbage by comparison with that of lowland pastures (6). The effect of lime and fertilizer applications were also well studied; the results of these and allied experiments have been recently reviewed in a station Bulletin (10).

In 1953 a Chemistry Section was established within the Station with the initial purpose of providing a routine analytical service for the plant breeders and agronomists. Research priorities were, however, quickly established as it became apparent that routine evaluation techniques were not always available or suitable for screening breeders' material. Initially, efforts were directed towards developing a more suitable method for predicting herbage digestibility than the conventional crude fibre method. In collaboration with workers at the Rowett Research Institute and the Grassland Research Institute, the normal acid fibre method was developed. Although the method was subsequently improved by increasing digestion time and introducing a pepsin digestion, it has now been superseded by the more convenient detergent fibre methods and, for predicting digestibility, by the more precise *in vitro* techniques. The normal acid fibre method sufficed, however, to show quite clearly that consistent variation existed between species and varieties in fibre content and, hence, presumably in digestibility (3); a conclusion now amply confirmed by both *in vivo* and *in vitro* digestibility studies.

A soil survey of the experimental land at Gogerddan was started in 1958 with the object of producing detailed maps showing micro-topography and soil properties. Soils were sampled at 15.25 m intervals and the nature of the parent material, drainage, depth and nutrient status was assessed. The maps derived from this survey have proved invaluable in showing the extent of variation and for the planning of field experiments. The soils fall into two groups, namely the brown earths and the gleys. Three soils series may be distinguished within the brown earths, two freely draining alluvial soils (Rheidol and Teify) and one derived from hard and soft shale drift material (Denbigh), and within the gleys, one poorly draining alluvial soil (Aeron) and two derived from hard and soft shale drift (Cegin and Sannan). The soils were found to be generally low in available calcium and magnesium and pH values ranged from 5-6.

Nitrate in herbage and its toxicity to the ruminant

One of the first research topics of the Department was the study of nitrogen accumulation in herbage. High levels of nitrate were observed in grasses and Brassicae, particularly in spring and autumn, even at moderate levels of nitrogen fertilizer. In general, nitrate was shown to accumulate when the supply of soil nitrogen exceeded that required for growth. Marked differences were found between grass species and varieties in their capacity to accumulate nitrate, cocksfoot varieties being invariably higher, for example, than ryegrass varieties (2).

The main interest of these results is in regard to the possible toxic effect of nitrate in ruminant feeding. Experiments in the United States had indicated the lethal level

of nitrate-N for ruminants to be 0.15-0.20%, while ap Griffith found levels as high as 0.6% in cocksfoot during autumn growth. Experiments with sheep showed that herbage containing up to 0.6% nitrate-N was not lethal or even harmful as far as could be ascertained by the absence of methaemoglobinaemia or associated symptoms. Feeding on hay containing 0.2% nitrate-N throughout tupping and pregnancy had no deleterious effect on fertility or the number or weight of lambs produced per ewe (15). Experiments at the Grassland Research Institute have shown no deleterious effects of even higher levels of nitrate on grazing lambs. It appears, therefore, that nitrate poisoning of sheep is unlikely under United Kingdom conditions, since the levels quoted in these experiments are in any event unlikely to be encountered in farm practice.

The anomaly between this conclusion and the currently accepted published levels of nitrate toxicity required investigation. Firstly, it should be noted that most of the experimental work in this country refers to sheep, and American evidence suggests that cattle may be more susceptible to nitrate poisoning. There appears, however, to be no well documented case of nitrate toxicity being reported in cattle in this country. A re-examination of the American literature on oat hay poisoning outbreaks revealed a second possibility. This showed that in almost every case of nitrate poisoning resulting from consuming oat hay, the hay which had been offered was either mouldy or damp. This suggests the possibility of nitrate being reduced to nitrite prior to its ingestion by the animal. The toxicity of nitrate depends on its reduction to nitrite by the rumen microflora, the absorption of this nitrite into the blood stream and a consequent methaemoglobinaemia. Since only a proportion of the nitrate is reduced in the rumen, it follows that nitrite is considerably more toxic than an equivalent amount of nitrate in the feed. Laboratory studies at the Station showed that when high nitrate grass was incubated overnight in water, considerable reduction of nitrate to nitrite occurred presumably as a result of the action of soil-microorganisms (8). Subsequent studies showed that appreciable quantities of nitrite were found when high nitrate hays were left outdoors for several days under wet conditions. In artificially dried grass no appreciable reduction of nitrate took place, presumably due to the heat sterilization of the microorganisms responsible. While pre-ingestion reduction of nitrate could easily occur under the hay-making conditions often encountered in this country, it is unlikely that hay crops would initially contain sufficient nitrate for appreciable quantities of nitrite to be formed.

There appears to be no evidence at present to substantiate the often repeated claims that disorders of stock grazing highly fertilized swards are due to nitrate poisoning. Herbage from such swards would, of course, be expected to contain appreciable amounts of nitrate, but unless clear symptoms of nitrate poisoning are also observed, it cannot be assumed that the ingestion of high nitrate grass is responsible for losses of stock. The possibility of sub-clinical effects of high nitrate ingestion must, however, be borne in mind and requires further investigation.

Soluble carbohydrates in grasses

Soluble carbohydrates form a very variable proportion of the dry matter in grasses,

ranging from as little as 2% to over 40%. It has been shown that considerable variation exists between grass species and varieties in soluble carbohydrate content when grown in the same environment. For example, soluble carbohydrates are particularly low in cocksfoot varieties and high in perennial and Italian ryegrasses, tetraploid varieties being usually higher than diploids. Soluble carbohydrate level is also very markedly reduced by the application of nitrogen fertilizer, presumably as a result of the more rapid growth due to nitrogen applications. Grasses which accumulate most nitrate-N when fertilized with nitrogenous fertilizers also show the lowest levels of soluble carbohydrates (7). In general, the application of nitrogen fertilizer will give a low soluble carbohydrate content in grass, accompanied by a high nitrogen content; when very high levels of nitrogen are applied to low soluble carbohydrate grasses, this may result in grass containing as little as 2% soluble carbohydrate and up to 30% crude protein. The nutritional significance of this situation requires investigation in view of the incidence of metabolic disorders in heavily fertilized pastures. Work in New Zealand, for example, has shown high protein grass to be associated with an increased rate of thermogenesis in cattle, leading to a lowered yield efficiency, while other workers have shown protein utilization to be improved by increasing the level of available carbohydrate in feeds. More evidence is, however, required before a valid assessment can be made on the effects of nitrogen fertilizers on herbage quality.

The ensiling characteristics of herbage species and varieties

The successful ensilage of herbage requires the production of sufficient lactic acid by bacterial fermentation to reduce the pH to a low level and to prevent undesirable fermentation. The substrate for lactic acid production is carbohydrate and it is reasonable, therefore, to expect that differences in soluble carbohydrate content between grass species and varieties may be reflected in their ensiling characteristics.

The extent of variation in the ensiling potential of herbages has been investigated during the past three years. Initially, efforts directed at evolving a small scale laboratory technique using plastic bags which are evacuated after filling with 100-200 g of fresh grass. Particular attention was given in the early stages of the investigation to the effects of nitrogen fertilizer applications on the ensiling behaviour of grasses. It is well established that such applications have marked effects on soluble carbohydrates and also that they often result in difficulties in silage making on the farm.

The results obtained showed considerable differences in the quality of silage made from different grass species and varieties, the differences being particularly marked at high levels of applied nitrogen. In primary growth cuts made in May, for example, perennial ryegrass varieties produced good quality silage, i.e. with no evidence of protein breakdown and absence of butyric acid, even at nitrogen levels as high as 200 kg N/ha. Cocksfoot varieties harvested on the same date produced silage of doubtful quality when 100 kg N had been applied, and a completely unacceptable product, high in ammonia and butyric acid, when 200 kg were applied to the sward. When this cocksfoot was supplemented with sucrose, silage of excellent quality resulted, indicating the deficiency to be one of available carbohydrate.

Two important conclusions follow from these results. Firstly, that the choice of variety is crucial in making good quality silage under intensive systems of growing grass when high levels of nitrogen fertilizer are applied. Secondly, the question of additives in silage making needs to be reassessed, taking into account the inherent differences in ensiling potential between varieties. For example, at high levels of nitrogen it appears that cocksfoot varieties require the addition of carbohydrate for satisfactory fermentation, whereas varieties of perennial ryegrass would not require such supplementation, except possibly in early spring and late autumn, when soluble carbohydrates are low in all grasses.

A direct relationship between soluble carbohydrate content and silage quality cannot be expected in view of the effects of other important factors, such as moisture content and buffering capacity. It appears from the results of the past three years, however, that a soluble carbohydrate content of over 10% is required before a satisfactory fermentation can be achieved with any degree of certainty. This is illustrated in the following table which compares silages made from S.37 cocksfoot ensiled with the addition of sucrose to increase the soluble carbohydrate content from 7.7% to the equivalent of 10, 15 or 20%.

Effect of different soluble carbohydrate (WSC) levels on silage quality

	Grass	Silage		
	%WSC	pH	% lactic acid	% butyric acid
original	7.7	5.6	0.83	3.0
adjusted	10	4.9	1.01	1.4
to:	15	4.4	1.05	0.2
	20	4.3	6.96	-

Increasing the soluble carbohydrate content clearly improved silage quality, as is seen from the decrease in butyric acid content.

Grasses low in soluble carbohydrates may also be presumed to give an acceptable product without additives if they are wilted prior to ensiling. The following table shows the effect of wilting on S.37 cocksfoot given 200 kg N/ha.

Effect of wilting on silage quality

	pH	%DM	% ammonia-N	% butyric acid
Unwilted	7.1	14	1.28	5.8
Wilted	4.9	20	0.43	0.8

While the wilted silage still contains appreciable quantities of butyric acid and ammonia, it is clearly a much better product than that from the unwilted grass.

Current experiments are mainly concerned with the problem of ensiling herbage at

difficult times of the year, such as late autumn, and assessing the advantage to be gained from the use of additives such as molasses and formic acid. The importance of buffering capacity in determining the ensiling potential is also being further investigated together with other factors which may make the ensiling of rapidly growing grass more difficult.

Digestibility and intake characteristics of herbage

The introduction of the two-stage in vitro digestibility technique (16) gave new impetus to the study of the nutritive value of herbage species and varieties, and the technique has been used extensively in the Station laboratories for the past eight years. In collaboration with the Grassland Agronomy Department the variation in grass species and varieties during primary growth and regrowth has been investigated with particular attention given to the interpretation of differences in digestibility between grasses in terms of growth stage and morphology (17). It has been shown, for example, that within a species almost all the variation in digestibility found between a range of different varieties in primary growth could be accounted for in terms of growth stage, proportion of leaf, etc. Between species, however, the differences could not be interpreted in this way, e.g. cocksfoot varieties are less digestible than ryegrass varieties at the same stage of growth, although higher in leaf content.

Other investigations have been concerned with the extent to which species or variety differences may be modified by management. It was found that a spring defoliation reduced the difference in digestibility between early and late cocksfoots by over 10 units when sampled in June, but had no effect on differences between early and late timothy varieties. Such a defoliation is common practice on many farms in the form of a spring grazing, and therefore requires to be taken into account in variety evaluation.

In vitro techniques have also proved useful in the interpretation of differences in the voluntary consumption of grass varieties by sheep. The low intake of timothy was related to a slow rate of digestion in vitro; significant variation was found between varieties and genotypes of timothy in the amount of dry matter digested in 24 hr (12).

Recently, the Grassland Agronomy Department has determined the voluntary intake of a large number of grass species and varieties at different stages of growth. The chemical composition and rate of digestion of these grasses have been examined with a view to establishing a reliable selection index for high intake characteristics which could be incorporated into a breeding programme. The correlations obtained between intake and various laboratory determinations are shown on p. 189.

The highest correlation with intake was obtained for 48 hr digestion in rumen liquor. None of the other determinations gave a correlation higher than that obtained for digestible organic matter. Improvements in the prediction of intake, possible through the estimation of other fibre constituents or their digestibility, are now being investigated together with the application of multiple correlations.

Correlation of voluntary intake with digestibility and chemical composition of grasses

	r value (n = 21)
Digestible organic matter	+0.85***
48 hr digestion with rumen liquor	+0.93***
Modified acid detergent fibre content	-0.86***
Pepsin solubility	+0.84***
Protein content	+0.68***

*** Significant at P = 0.001

Animal experiments at the Station have clearly shown that differences in voluntary intake occur when sheep and cattle are offered different grass varieties at the same level of digestibility (11). The development of a suitable laboratory scale technique for predicting voluntary intake is, therefore, of high priority if quality breeding programmes are to be meaningful.

The mineral content of grasses in relation to nutritional requirements

Considerable variation exists in mineral content between different grass species and varieties. For many elements much of this variation is associated with the difference in the proportion of leaf or stage of growth. Sodium content, however, appears to show inherent variation which is independent of growth stage or morphological characteristics. Varieties of timothy and meadow fescue, for example, are consistently lower in sodium content than varieties of cocksfoot and ryegrass (4). Similarly, consistent variation has been noted between varieties within a species, such as perennial ryegrass, even when they are grown in soils of different sodium content.

The level of several nutritionally important elements found in grasses at fairly mature stages of growth is frequently below the estimated minimal requirement of stock although the intake and digestibility of the grasses are sufficiently high to sustain high levels of animal production. The following table compares the content of some essential minerals in grasses harvested at a dry matter digestibility of 70%, with the specified requirement for sheep and cattle (1).

Mineral content of grasses and nutritional requirements (% in DM)

	P	Ca	Na	Mg
S.37 cocksfoot	0.29	0.25	0.75	0.09
S.24 perennial ryegrass	0.25	0.25	0.60	0.09
S.170 tall fescue	0.20	0.27	0.42	0.17
S.51 timothy	0.17	0.28	0.03	0.08
Requirements				
Cow yielding 10 kg milk/day	0.42	0.52	0.15	0.15
Sheep gaining 200 g/day	0.25	0.50	0.07	0.06

On the basis of these requirements, none of the four grasses would supply sufficient phosphorus or calcium to meet the requirements of a milking cow. The estimated requirements do, of course, include a safety margin and deficiencies could not be recognized until lower levels were reached. In this respect there is little experimental evidence available to allow an accurate assessment of the nutritional adequacy or otherwise of grass diets when offered without supplementation with either concentrates or mineral mixtures.

In experiments with mature wethers it was found that feeding S.51 timothy (0.04% Na) resulted in a rapid reduction in saliva sodium and a corresponding rise in saliva potassium, leading to an abnormal Na:K ratio. Negative sodium balances also occurred; these were corrected, as was saliva composition, by the addition of sodium salts to the timothy diet (9). In a subsequent experiment, sheep grazing timothy pasture showed changes in saliva composition within a week of being turned out to pasture, while sheep on ryegrass pasture maintained a normal saliva composition. Weight gains were not significantly different on the two pastures. Low levels of sodium may, however, impair the performance of lactating ewes or dairy cattle, as indicated by the work done in Holland, where a response in milk yield was obtained through sodium supplementation of low sodium diets.

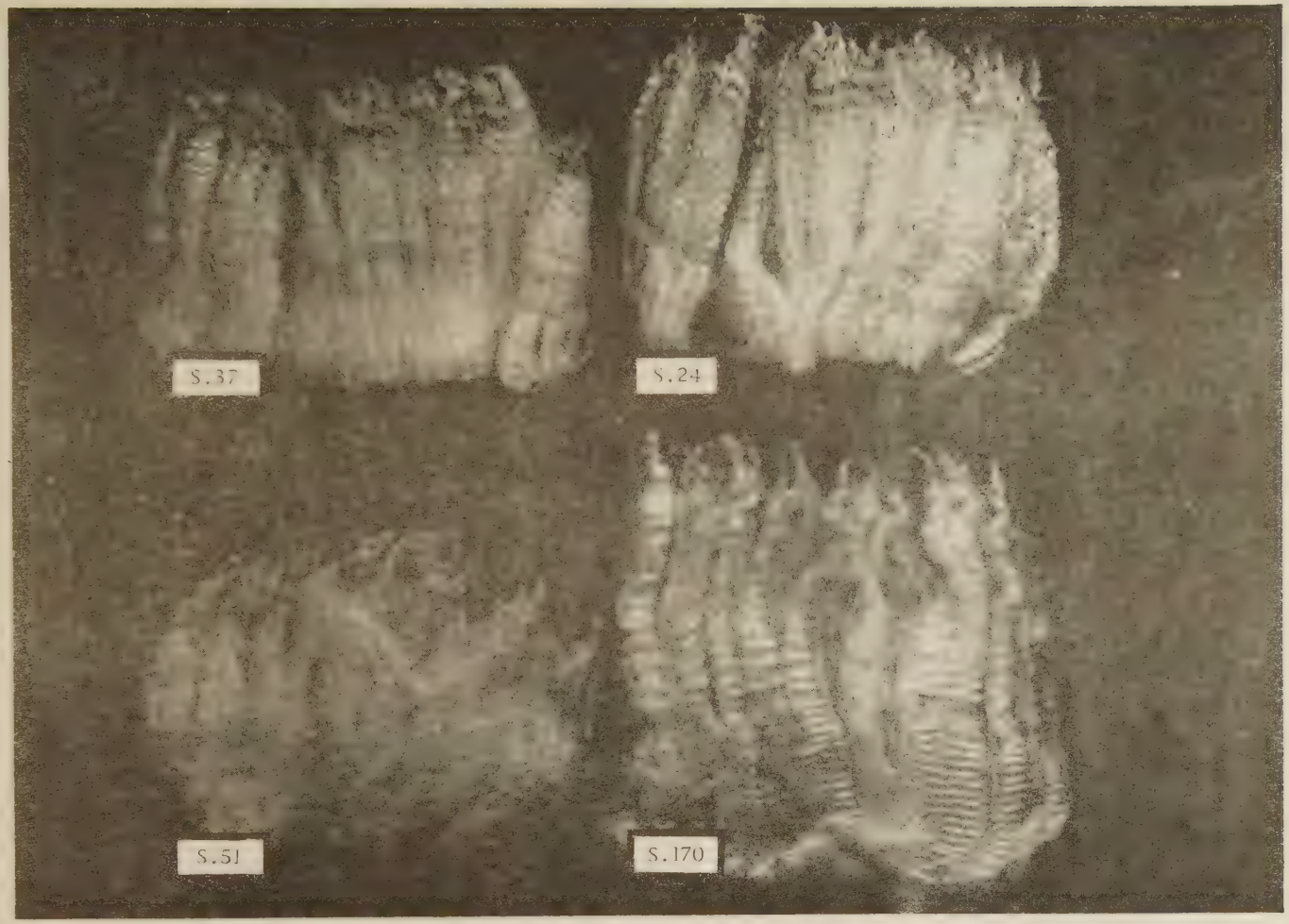
Low levels of nutritionally important trace elements, such as copper, cobalt and iodine, have also been found in grass varieties, particularly at mature stages of growth. Significant variation was again found between species and varieties as exemplified in the table below for copper content (unpublished data).

Copper content of grasses (mean of 2 cuts; ppm in DM)

S.23 perennial ryegrass	5.4
S.24 perennial ryegrass	6.1
S.321 cocksfoot	5.8
S.345 cocksfoot	7.2
S.37 cocksfoot	8.5
S.48 timothy	6.4
S.51 timothy	5.2
Least signficant difference (P = 0.05)	1.05

The levels of trace elements are again frequently lower than the published standard of 10 ppm copper for cattle, a level not attained in any of the grasses listed in the above table.

In the course of feeding experiments with lambs, symptoms of copper deficiency were noted, namely depigmentation of hair and loss of wool crimp. These were observed in lambs offered S.51 timothy and, to a lesser extent, S.24 perennial ryegrass, but not in lambs offered S.170 tall fescue or S.37 cocksfoot (13). In a second experiment the symptoms of copper deficiency again occurred, this time in lambs offered S.352 timothy, but did not occur in similar lambs offered S.48 timothy, although both



Influence of herbage feeds on wool characteristics

grasses contained over 6 ppm copper, a level which would be considered nutritionally adequate in weight gain.

In the same experiments, positive responses in weight gain followed cobalt supplementation, although cobalt levels were generally higher than the estimated requirement. Serum B_{12} analyses carried out by the N.A.A.S. confirmed the inadequacy of the diets with respect to cobalt. The results from these experiments suggest that the availability of trace elements may be low in certain varieties and requires further investigation (14).

The adequacy of a herbage to supply sufficient iodine to meet dietary requirements is complicated by the presence in certain crops of thiocyanate-yielding thioglucosides which impair normal thyroid function. Investigations in collaboration with the Arable Crops Section showed high levels of thiocyanate to occur in the young tissues of certain kale varieties. Other varieties contained much less thiocyanate, indicating the possibility of selecting low-thiocyanate lines. Experiments with sheep showed that the ingestion of feeds supplemented with thiocyanate to levels similar to those found in kale, led to reduced thyroid uptake of ^{131}I.

FUTURE DEVELOPMENTS

Improvements in the techniques of pasture evaluation in the past decade have made the breeding of herbage plants for nutritive quality a realizable objective. At the same time progress has been made through animal experimentation in defining the characteristics of herbage which limit animal production, thus permitting a more logical and precise approach to the evaluation of herbage quality.

At the present time progress is being made in selecting herbage plants with a higher digestibility. The need to associate this improvement with a commensurate improvement in intake characteristics is now becoming apparent through animal experimentation. Considerable research is therefore being directed at this and at other research centres towards reaching a better understanding of the factors influencing the voluntary intake of herbages by ruminants, and towards the development of screening techniques for improving intake which would be suitable for use in the breeding programmes. It is likely that the next major advance will result from the application of screening techniques, fully evaluated in animal experiments, which will facilitate selection for both high digestibility and high intake characteristics.

The development of new varieties capable of higher levels of animal production may well accentuate various metabolic disorders in stock, often associated with more intensive systems. It is important, therefore, that the significance of organic and inorganic constituents of herbage which may impair feed utilization is not overlooked. The mineral status of grass varieties, in particular, appears to be inadequate to meet the requirements of the ruminant at high levels of production. In this respect little progress has been made in our understanding of the way in which inorganic elements occur naturally in the plant. There are indications from animal experiments that the

availability of certain inorganic elements varies between herbage varieties, indicating the need to investigate more fully the chemistry of these constituents in plants.

Crop conservation is also likely to feature more predominantly in animal production in the future. While much of the increase in conservation will be artificial drying, high priority should also be given to ensilage which allows to conserve high quality herbage at minimum cost. The factors which influence the ensiling characteristics of varieties need systematic study, and the advantage of breeding varieties specifically suited for conservation needs to be compared with that of using chemical additives to achieve satisfactory preservation.

Quality considerations have long been a feature of cereal breeding programmes designed to produce varieties suitable for malting and brewing. In recent years the nutritive quality of cereal grain is also being increasingly considered in breeding programmes. Both an increase in the protein content of cereals and an improvement in the balance of amino acids in the proteins will enhance the feeding value of cereals. Such improvements offer considerable scope for the plant breeders when suitable evaluation techniques are established. Total protein may be determined on large numbers of samples by automated Kjeldahl procedure, but it is difficult to screen for protein quality. Measurement of dye-binding capacity has been found to give an estimate which correlates with both quantity and quality of protein, but methods of assaying individual amino acids, although available, are not well developed for use as screening techniques. However, techniques are available for the detailed study of the composition of cereal proteins on a limited scale. Preliminary research is now being undertaken on the effect of genetic and environmental factors on protein composition, with the object of assessing the potential and the feasibility of improving protein quality in cereals.

References

(1) Agricultural Research Council 1965, The nutrient requirements of farm livestock, No.2. ARC London.

(2) G.ap Griffith, 1958, Nature, Lond. 182, 1099.

(3) G.ap Griffith and J.P.Cooper, 1959, J.Br.Grassld Soc. 14, 272.

(4) G.ap Griffith and R.J.K.Walters, 1966, J.agric.Sci., Camb. 67, 81.

(5) T.W.Fagan and H.T.Jones, 1924, W.P.B.S.Bull.Series H.No.3, 85.

(6) T.W.Fagan and R.O.Davies, 1937, Proc.4th Int.Grassld Congr., Aberystwyth 370.

(7) D.I.H.Jones, G.ap Griffith and R.J.K.Walters, 1961, J.Br.Grassld Soc. 16, 272.

(8) D.I.H.Jones and G.ap Griffith, 1965, J.Sci.Fd agric. 16, 721.

(9) D.I.H.Jones, D.G.Miles and K.B.Sinclair, 1967, Br.J.Nutr. 21, 391.

(10) Ll.Iorwerth Jones, 1967, Studies on Hill Land in Wales, Technical Bull.No.2 Welsh Plant Breeding Station, pp.179.

(11) D.G.Miles, R.J.K.Walters and E.Evans, 1968, Anim.Prod. 11, 19.

(12) B.D.Patil, 1969, Ph.D.Thesis, Univ.Wales (unpublished).

(13) B.D.Patil, D.I.H.Jones and R.Hughes, 1969, Nature, Lond. 223, 1072.
(14) B.D.Patil and D.I.H.Jones, 1970, Proc.11th Int.Grassld Congr, Brisbane (in press).
(15) K.B.Sinclair and D.I.H.Jones, 1964, Br.Vet.J. 120, 78.
(16) J.M.A.Tilley and R.A.Terry, 1963, J.Br.Grassld Soc. 18, 104.
(17) R.J.K.Walters, G.ap Griffith, R.Hughes and D.I.H.Jones, 1967, J.Br. Grassld Soc. 22, 112.

CYTOLOGY

P.T.THOMAS
HUGH THOMAS

Cytological studies at the Station have generally been directed to be of immediate value to the plant breeder, and the work has been concentrated on those species which are of particular importance in the breeding programmes. In the first instance, the establishment of chromosome numbers of material largely introduced from plant collections is necessary, and this is then further screened as basic material for breeding. Further investigations on selected material have aimed at determining the chromosome constitution and genetic architecture of related species with the object of creating new variability through chromosome manipulation.

Of the grasses, the genus Dactylis and the Lolium/Festuca complex have received the greatest attention and, more recently, an extensive study has been made on the cytogenetics of Avena.

Dactylis

The chromosome numbers of a whole range of indigenous and introduced material have been determined and a chromosome atlas showing the distribution of chromosome races of Dactylis has been produced (7, 1). Diploid, tetraploid and hexaploid races have been recorded. Chromosome pairing in the two polyploid races indicates that both are autopolyploid in origin. The high incidence of multivalents manifests the similarity in the duplicated chromosome sets. Dactylis glomerata, the cultivated cocksfoot, is a tetraploid species, and studies of chromosome relationships between the tetraploid and diploid species have indicated possible pathways for introducing genetic variation from the diploid into the tetraploid.

F_1 hybrids between different diploid sub-species have regular chromosome pairing and no evidence of gross structural differences in chromosome complements of the sub-species was obtained from a study of the meiotic behaviour of the F_1 hybrids. However, in spite of this regular meiosis, the F_1 hybrids show a reduction in their fertility compared with the sub-species.

Triploid hybrids between diploid and tetraploid species showed a characteristic autotriploid behaviour, with trivalents being the predominant associations. On back-crossing, the triploids were partially female fertile, crosses to the tetraploid being twice as successful as to the diploid (8). Plants with 27 and 28 chromosomes were the

most frequent in the progeny of triploid hybrids crossed with tetraploids. The meiotic behaviour of these backcross progeny was similar to the natural tetraploids and they were also relatively fertile. The triploid hybrids function as a bridge in the flow of genes from the diploid to the tetraploid species and their introgression would enrich the genetic variation of the natural tetraploids. The recovery of fertility after one backcross could be used by the plant breeder to introduce genes from the diploid species into the tetraploids.

Another method, whereby the diploid genes could be transferred into the tetraploid pool, has been described by Carroll and Borrill (2). Chromosome counts of the crosses between diploid and tetraploid species show that tetraploid hybrid progeny are produced as frequently as the expected triploids, but the relative proportions of triploid and tetraploid hybrids seem to be dependent on the parental genotypes used in the crosses. The mechanism involved in the production of tetraploid hybrids could be due to nonreduction or to double fertilization. The data available are insufficient to differentiate unequivocally between these two possibilities. However, the evolutionary significance of this mechanism is obvious, and it also offers the breeder the opportunity of utilizing any desirable genetic variation in the diploid species with the minimum amount of hybridization.

Lolium/Festuca

Lolium species are essentially diploid, but successful autotetraploid varieties have been produced, although they have the disadvantage of having a relatively low dry matter content. They are reasonably stable at a high level of quadrivalent formation, and fertility has been found to be associated with selection for regular disjunction at meiosis.

A major breeding objective has been to combine the desirable agronomic and nutritive features of L. multiflorum with the persistence of L. perenne. At the diploid level the chromosomes of the species are sufficiently homologous to pair regularly in early generations, but genetic influences lead to instability in later generations.

For these reasons the breeders have concentrated on the production of allotetraploids between the two species. In the first generation in such allotetraploids the number of quadrivalents indicates a degree of preferential pairing but in subsequent generations, in contrast to the situation in autotetraploids, there is a progressive reduction in quadrivalent frequency. Thus, while an autotetraploid variety achieves stability at over four quadrivalents per nucleus, in the allotetraploid there is a progressive reduction from just over two quadrivalents in the first to less than one in the fourth generation.

These cytological studies emphasize the problem of obtaining and stabilizing desirable combinations of characters from the two species. Thus in the diploid hybrid recombination is possible due to interspecific chromosome pairing accompanied by instability, whereas the position in the allotetraploid is that stability has been achieved, but the opportunity for recombination has been greatly reduced. More effective breed-

ing will, therefore, have to be concerned with two alternatives, the one of doubling the chromosome number of desirable segregates from the diploid hybrid, and the other, of substituting individual chromosomes into the allotetraploid.

Recent studies in Festuca pratensis have revealed the importance and significance of chromosome differentiation in the synthesis of new forms (3). A naturally occurring tetraploid form of F. pratensis from Switzerland was crossed with the diploid S.215 variety of the same species. Cytologically, the triploid has shown good pairing between the three sets of chromosomes, but the synthetic hexaploid derivative had regular meiosis with a very low proportion of quadrivalents, and was fully fertile. It is concluded that the three sets of chromosomes are sufficiently differentiated from each other for random pairing to occur between the "homologous" chromosomes in the triploid and to encourage preferential bivalent pairing in the hexaploid. There is also some evidence that a genetic control of chromosome pairing in the hexaploid is involved. Thus it appears possible to produce stable and attractive synthetic hexaploids by combining genomes of the same or closely related species which show appropriate degrees of differentiation (25).

The normally hexaploid species F. arundinacea has been found to have a higher biological potential than any of the temperate grasses, but again it is desirable to introduce favourable characteristics from Lolium. To establish the chromosome constitution and genetic architecture of F. arundinacea, an extensive series of hybrids and amphiploids involving related species of Festuca were produced and studied cytologically by C.P. Malik (9-12) and P. Chandrasekharan (3). Further studies have been made on the amphiploid between L. multiflorum and F. arundinacea and its derivatives produced by E.J. Lewis.

From the species and hybrids available for study in the F. arundinacea group the following classification for chromosome constitution is suggested:

Species	Genomic designation
Festuca pratensis	PP
F. mairei	$M_1M_1M_2M_2$
F. arundinacea var. glaucescens	$G_1G_1G_2G_2$
F. arundinacea var. genuina	$P_AP_AG_1G_1G_2G_2$
F. arundinacea var. atlantigena f. pseudo-mairei	$G_1G_1G_2G_2M_1M_1M_2M_2$
F. arundinacea var. letourneuxiana	$P_AP_AG_1G_1G_2G_2M_1M_1M_2M_2$

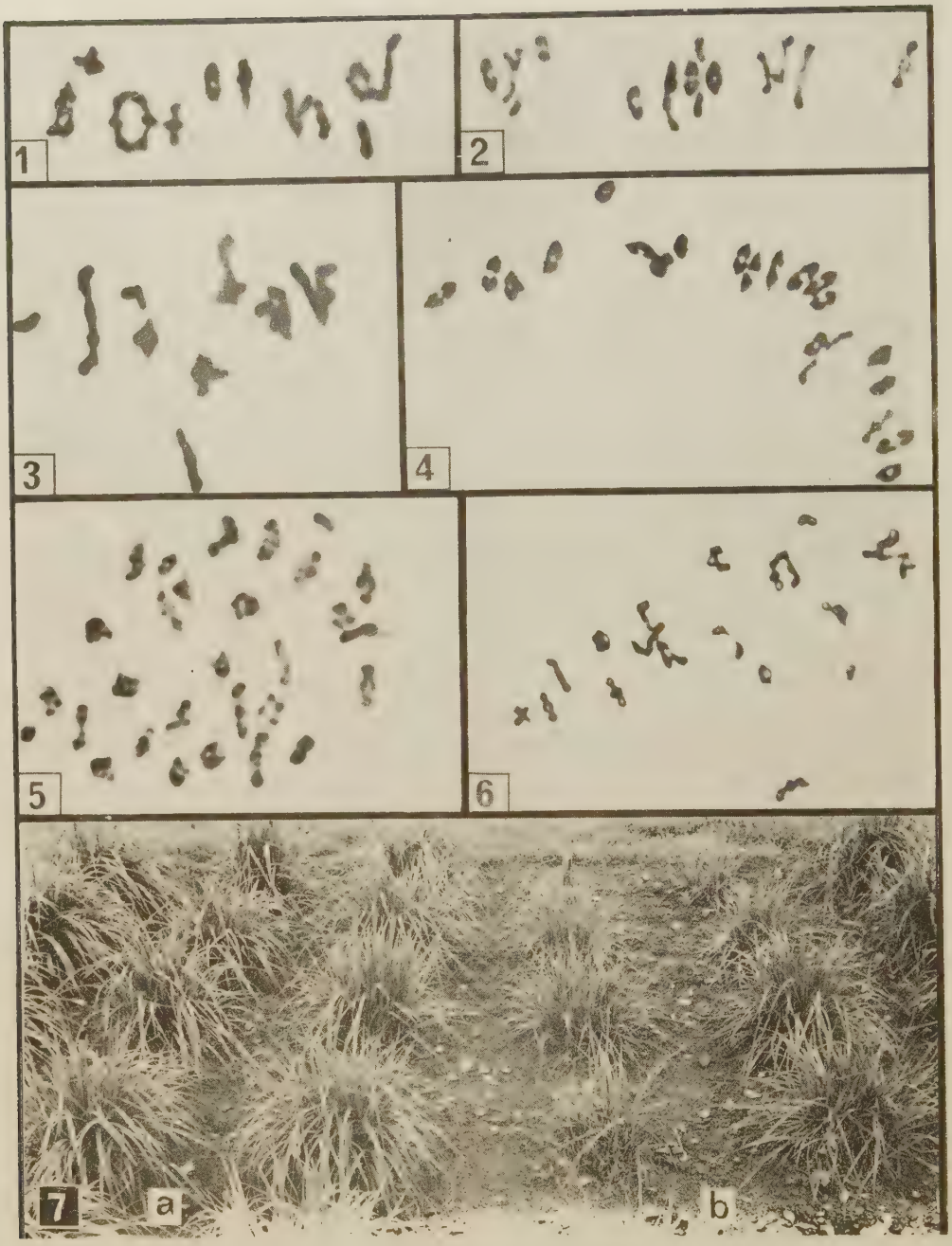


Plate 1.

1. Allotetraploid between Lolium perenne and L. multiflorum (F_1). 2. F_4 derivative. 3. Triploid between tetraploid Festuca pratensis and diploid S.215. 4. Hexaploid derivative. 5. Amphiploid between F. arundinacea and L. multiflorum. 6. Backcross to tetraploid L. multiflorum. 7. Synthetic hexaploid F. pratensis (a) compared with diploid S.215 (b).

This information, in association with our knowledge of the chromosome relationships between the diploid Lolium species, enables us to suggest appropriate pathways for the production of new synthetic species, which in association with other methods of chromosome manipulation will lead to the development of new types of improved grass varieties. The production of polyploids in these grasses has been greatly facilitated through the development of a technique by J. Clarke (4) which involves synchronization of mitotic divisions by 5-amino-uracil before treatment with colchicine.

Attempts by E.J. Lewis to introduce genomes of L. multiflorum into the hexaploid F. arundinacea have been reasonably successful. The amphiploid involving these two species gives a range of plants which have fairly regular chromosome behaviour at meiosis and high pollen fertility. Backcrosses between the amphiploid and tetraploid L. multiflorum show meiotic behaviour in accordance with their suggested genomic constitution and are sufficiently fertile to make possible a successful selection for desirable agronomic characteristics in future generations.

The production of haploids followed by duplication of the chromosome number is a desirable objective, both for genetical studies, and for the immediate production of homozygotes. Some success has already been achieved in a Festuca/Lolium hybrid, and D.H. Clapham is concerned with increasing the frequency of success and with developing the technique for a wide range of material. Associated with this work, a method for the clonal multiplication of kale by tissue culture has been developed. This enables about 200 plantlets to be grown from slices of petiole from the parent plant.

Avena

As a corollary to the breeding programme in oats, cytogenetic investigations aimed at elucidating the genomic architecture of cultivated hexaploid oats have been and are being currently undertaken at the Station. Initially, our effort was concentrated on the cytogenetic behaviour of species hybrids within the genus Avena in an attempt to trace the wild diploid progenitors of the cultivated forms. This work is still in progress and a parallel approach has been started using aneuploids for the monosomic analyses of the cultivated oat.

Cytogenetic investigations in the Avenae were initiated in the early 1950s by D.J. Griffiths and his colleagues (6). Hybrids between diploid and tetraploid species were the first to be produced. These triploids were subsequently treated with colchicine to form synthetic hexaploids, and these were crossed with the cultivated hexaploid A. sativa. Chromosome pairing in all the hybrids and amphiploids confirmed the earlier Japanese work that the A genome of strigosa was related to one of the genomes of the tetraploid and hexaploid species. The second genome of the tetraploid species did not occur in the hexaploid. From these studies it was established that the genomic formulae of the diploid, tetraploid, and hexaploid species were AA, AABB and AACCDD respectively. Furthermore, this work also showed conclusively that the diploid species A. strigosa, A. hirtula, A. brevis, A. nudibrevis and A. wiestii were identical in chromo-

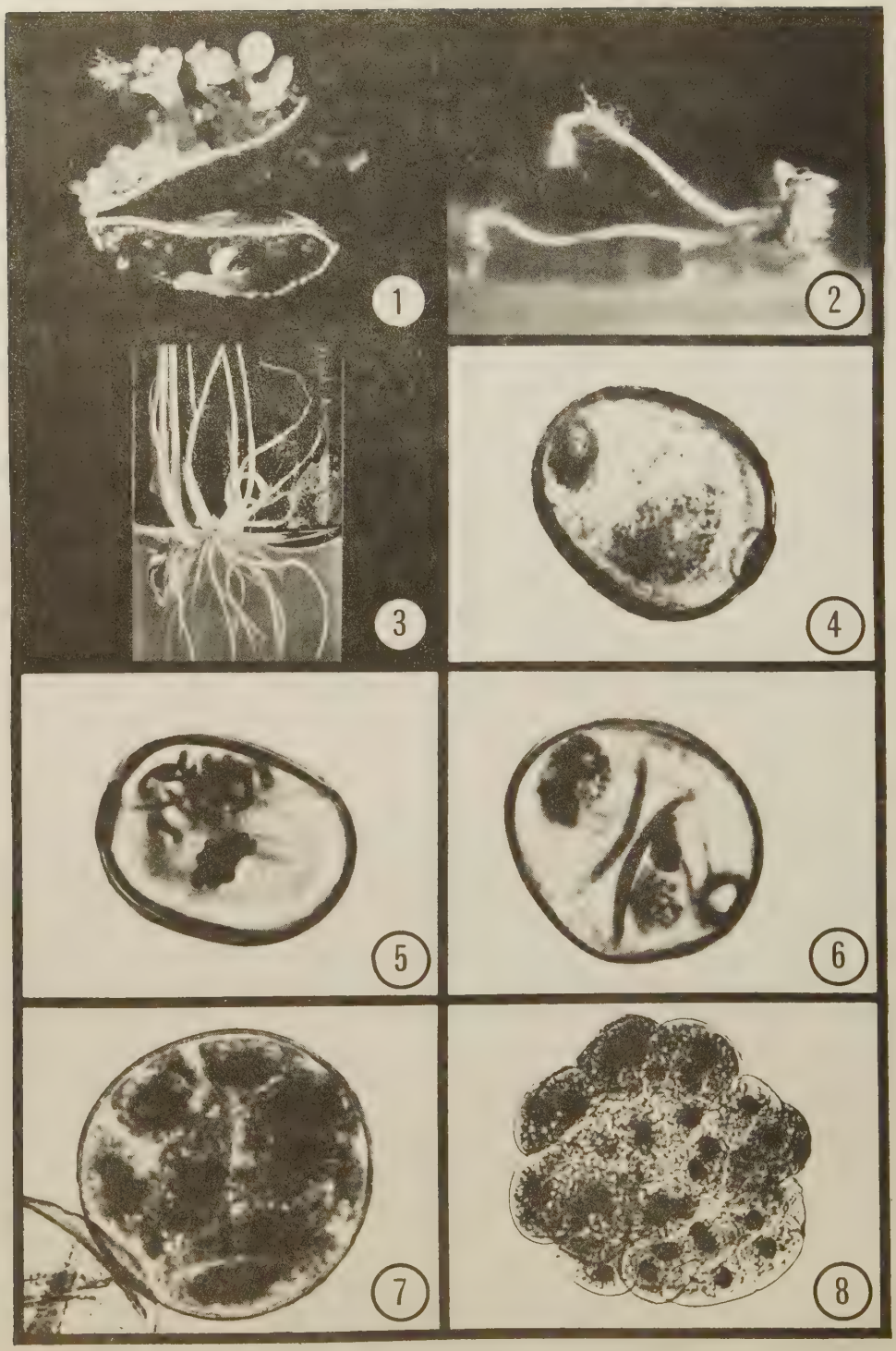


Plate 2

LEGENDS TO PLATE 2

1. Plantlets growing *in vitro* from an anther of *Nicotiana tabacum*.

2. Callus and roots from an anther of a *Festuca-Lolium* hybrid.

3. Plant from an anther of *Lolium multiflorum*.

4. Differentiating pollen, *in vivo*, showing vegetative and generative nuclei after first pollen grain mitosis typical of Gramineae.

5-8. Successive stages in the development of pollen in anthers cultured *in vitro* on a high sucrose medium for 6-14 days.

   5. Pollen grain with two mitotically active nuclei slightly out of phase (*Lolium multiflorum*).

   6. Pollen grain with distinctive pairs of nuclei (*Lolium multiflorum*).

   7. Multicellular pollen grain, exine and intine still visible (*Hordeum vulgare*).

   8. Callus from a pollen grain after bursting of the exine (*Hordeum vulgare*).

SELECTED REFERENCES TO OTHER WORK

Guha, S. and Maehshwari, S.C. (1966) Nature, Lond. 212 (5057), 97-98 (*Datura*).

Niizeki, H. and Oono, K. (1968) Proc. Japan Acad. 44, 554-557 (*Oryza*).

Nitsch, J.P. and Nitsch, C. (1969) Science 163, 85-87 (*Nicotiana*).

Sunderland, N. and Wicks, F.M. (1969) Nature, Lond. 224 (5225), 1227-1229 (*Nicotiana*).

Nitzsche, W. (1970) Die Naturwissenschaften 4, 199-200 (*Festuca-Lolium*).

Sharp, W.R. (1970) Pers. comm. (*Lycopersicon*).

some structure, since hybrids produced between any two species regularly formed seven bivalents and were completely fertile. The only other diploid species available at that time, A. longiglumis, was shown to differ from the strigosa group by a number of translocations. F_1 hybrids between A. longiglumis and any member of the strigosa group were sterile as a result of the highly irregular meiosis (4).

The earlier work was hampered by the non-availability of a number of described species of Avena. This was corrected to a large extent by a joint Canada/Wales plant collecting expedition to the Mediterranean region in 1964. Genotypes of the three diploid species A. pilosa, A. clauda and A. ventricosa became available for cytogenetic studies as a result of this collection. A. pilosa and A. clauda are closely related, and hybrids between them regularly form seven bivalents (15). A. ventricosa differs from clauda-pilosa by at least three major translocations, and consequently the F_1 hybrids are sterile. Thus far, every attempt to hybridize any of these species with the strigosa group has been unsuccessful; karyotypically they differ from the strigosa group in that they have predominantly sub-terminal chromosomes. Divergence in the diploid species of Avena has taken place along two parallel pathways, one to develop the strigosa group and its offshoot longiglumis, and the other to form the pilosa-clauda complex and its modified form A. ventricosa.

It soon became apparent in the cytogenetic investigations of the Avenae that the three tetraploid species described prior to 1968, namely, barbata, abyssinica, and vaviloviana were genomically identical. Another acquisition from the Mediterranean collection was a new sterilis-like tetraploid which has been subsequently named A. magna (13). The significance of this tetraploid form has been discussed by Rajhathy and Sadisavaiah (17), and it may be an important link in the evolution of the hexaploid forms.

The meiotic behaviour of hybrids between hexaploid species of Avena, namely sativa, byzantina, nuda, fatua, sterilis and ludoviciana, demonstrate clearly that all the hexaploid species have the same genomes, the F_1 hybrids form 21 bivalents and are fertile. No barriers to free gene flow between hexaploid species exist, and the results of cytogenetic investigations undertaken by D. J. Griffiths and his colleagues(unpubl.) on hexaploid hybrids indicate that the status of sub-species would be more appropriate for these hexaploids. The hexaploids represent one genetic species, and morphological differences delineating taxonomix species are controlled by single genes. Free gene flow between hexaploid species, without any disturbance in chromosome behaviour, has been exploited in the transfer of a mildew resistant gene from A. sterilis into cultivated background, resulting in the variety Mostyn.

From the earlier investigations it became readily apparent that the Avena material available prior to the Mediterranean collection did not contain the diploid progenitors of the C and D genomes of the hexaploids. Rajhathy (16) proposed that the diploid species A. ventricosa was a possible progenitor of the C genome of the hexaploids. The F_1 hybrid between ventricosa and sativa and the derived amphiploid have been studied recently and the results confirm Rajhathy's hypothesis that ventricosa is related to the

C genome of A.sativa (24). The cytogenetic data are confirmed by electrophoretic studies of the protein patterns of Avena species (22). Therefore the diploid progenitors of two of the hexaploid genomes have now been identified.

Numerous amphiploids derived from treating F_1 interspecific hybrids with colchicine have been synthesized at the Station since the initiation of the Avena cytogenetic programme. The cytological behaviour of these amphiploids is summarized in Table 1. Compared with the octoploids and decaploids, the synthetic hexaploids have a higher frequency of multivalents which would be in agreement with a genomic formula of AAAABB. Differential pairing between chromosomes of the same origin in the octoploid and decaploid amphiploids results in a preponderance of bivalents. Since the bivalents formed are homogenetic, segregation and recombination of characters introduced from either parent into the amphiploid is minimal in filial generations of the amphiploids. On the other hand, the more autopolyploid-like meiotic behaviour of the synthetic hexaploids allows for considerable segregation and recombination of diploid and tetraploid genes at the hexaploid level. The cytogenetic behaviour and fertility of these amphiploids demonstrate conclusively that the production of new species by combining the genomes of natural species would not be a practical approach in the improvement of the oat crop. Nevertheless these amphiploids could be used as bridges for the transfer of genes from wild species into the cultivated oat A.sativa (22).

In more recent years our efforts have been concentrated on investigations which yield more precise information on genetic relationships between species of Avena and eventually the genomic architecture of the cultivated oat A.sativa (18, 23, 24). This approach has been stimulated by the isolation of wild species of Avena with attributes whose introduction into the cultivated forms would be desirable, in particular resistance to various diseases. In order to use this new source of untapped variation it is essential to define the genetic relationships between species of lower ploidy and the hexaploids.

Table 1. Chromosome pairing and fertility of synthetic amphiploids

Amphiploid	Chromosome number	Mean number per cell I	II	III	IV	Fertility
A.barbata x A.hirtula	42	2.17	14.34	1.50	1.39	40.37
A.abyssinica x A.strigosa	42	1.55	13.90	1.05	2.35	-
A.barbata x A.longiglumis	42	2.30	11.85	2.20	1.85	26.40
A.hirtula x A.sativa	56	1.56	25.50	0.20	0.21	84.3
A.pilosa x A.sativa	56	0.75	27.05	0.17	0.01	-
A.ventricosa x A.sativa	56	0.02	27.65	0.01	0.04	-
A.abyssinica x A.sativa	70	2.93	32.35	0.23		10.28

Hybrids between A.sativa and each of the four diploid species, A.hirtula, A.longiglumis, A.pilosa and A.ventricosa, have been produced. Chromosome pairing in the

F_1 hybrids shows that the diploid genomes are related to one of the hexaploid genomes, hirtula and longiglumis to the A genome, and pilosa and ventricosa to the C genome (18, 19, 24). However, this homology was not readily apparent in the derived amphiploids since they were nearly completely bivalent pairing on account of differential pairing between true homologues. In hybrids between the octoploid amphiploids and A. sativa, which combine the sativa complement and the haploid set of the diploid species, the diploid chromosomes fail to pair with their equivalent pair in sativa. The chromosomes of the diploid progenitors of the hexaploid A and C genomes have become differentiated from the A and C genomes of A. sativa.

Since the diploid chromosomes remained unpaired in the hybrids between the octoploids and A. sativa, progenies derived from selfing these genotypes vary in chromosome number from 42 to 49, the majority falling in the 42-44 range due to the selective elimination of hyperploid gametes. Progenies with 43 chromosomes are of great interest in that they combine the sativa complement and a single chromosome of the diploid species. Six of the possible seven single chromosome addition lines of A. hirtula to A. sativa have been identified and described (23). Chromosome pairing in these six lines revealed that the chromosomal differentiation that has occurred between the diploid and hexaploid A genomes is not homogeneously distributed throughout the complement, some hirtula chromosomes pairing more readily than others with their sativa equivalents. Similarly, the fertility and stability of the addition lines were also dependent on the hirtula chromosome involved. A number of single chromosome addition lines of pilosa and ventricosa to sativa have been isolated, but their classification is not yet complete.

Chromosome differentiation has played a significant role in speciation in Avenae, and the variation in chromosome structure at the diploid level is pronounced in such a limited group. Considerable diversity in chromosome structure is found within the hexaploid karyotype, and it is possible to classify the chromosomes into four groups, viz. satellite, median, sub-median and sub-terminal. Divergence in chromosome structure would be in agreement with the presumed allopolyploid origin of hexaploid oats. However, the meiotic behaviour of a nullihaploid reported by Gauthier and McGinnis (5) indicates that bivalent pairing in hexaploid species is not entirely dependent on differential affinity. More chromosome pairing in the nullihaploid compared with an euhaploid of sativa reported by Nishiyama and Tabata (14) demonstrates the presence of a genetic system suppressing homoeologous pairing in the hexaploids. The meiotic behaviour of the amphiploids combining diploid and hexaploid genomes of Avena studied by us, shows the importance of the sativa genome in controlling chromosome pairing (18, 19, 23, 24). The precise analysis of the mechanism controlling bivalent pairing in A. sativa forms an important part of the present cytogenetic programme. The elucidation of this mechanism is essential for the proper understanding of the genomic structure of the hexaploids.

The evolution of the hexaploid oat arising from the combination of three distinct basic genomes, and their integration into a chromosomally stable genotype, means that the hexaploids can tolerate aneuploid genotypes in their progeny on account of the genetic duplication inherent in such a genomic structure. Tolerance to chromosome

loss enables us to isolate monosomic lines from varieties of cultivated oat A.sativa. A number of monosomic lines have been identified in the variety Manod, and we have also received a number of monosomic lines from other research laboratories.

These lines are being used to map genes on specific chromosomes by means of monosomic analysis. Studies have also been started on monosomic-tetrasomic analysis to identify homoeologous groups within the hexaploids. Telocentric chromosomes arising from the loss of one of the arms of the monosomes have been isolated from the progenies of monosomic lines. These marked chromosomes will be invaluable in identifying the chromosomes of each of the three genomes of sativa. In view of the importance of a monosomic series, considerable attention is given to establishing the complete series of monosomic lines, since this will eventually lead to greater precision in defining relationships between constituent genomes of sativa than would the study of the meiotic behaviour of interspecific hybrids.

The ultimate objective of the cytogenetic investigations on speciation in the Avenae and on the genomic architecture of A.sativa is the evolution of techniques for the transfer of desirable genes from wild species of lower ploidy into the cultivated oat. Recently, emphasis has been placed on developing pathways for the transfer of mildew resistant genes from the two diploid species A.hirtula and A.ventricosa and from the tetraploid species A.barbata into A.sativa. The most promising approach based on cytogenetic investigations is to isolate 43-chromosome lines constituting the sativa genome and the single alien chromosome on which the gene is located. In these genotypes the alien chromosome occasionally forms a trivalent with its equivalent pair in sativa, and hence some recombination between the diploid chromosome and the corresponding chromosomes in the hexaploid should take place. Resistant plants amongst the progeny of these 43-chromosome plants could be monosomic addition lines(2n=43), disomic addition lines (2n=44) and euploids (2n=42). The latter group would be recombinants or chromosome substitutions. Once established in an euploid genotype, the transferred gene could be introduced into any variety by a series of backcrosses. Large populations of selfed progenies from 43-chromosome lines of the hirtula, ventricosa, and barbata genes are being screened for mildew resistance by members of the Arable Crop Department.

Although all three wild species are completely resistant to the prevalent races of mildew, this degree of resistance is not recovered in 43-chromosome lines. The hirtula resistance is not effective at the seedling stage in monosomic addition lines and is more characteristic of adult plant resistance. The ventricosa and barbata resistance is more effective at the seedling stage, although the complete resistance of the wild species is not recovered in sativa background. The barbata resistance is the most effective and shows a characteristic necrotic effect in sativa background. Since these are the only available sources of resistance to prevalent races of mildew, their introduction into the cultivated A.sativa is of immediate importance. The elucidation of the genomic structure of the cultivated oat will result in the development of more precise techniques for the introduction of alien variation into cultivated oat and therefore augment the present gene pool available to the plant breeder.

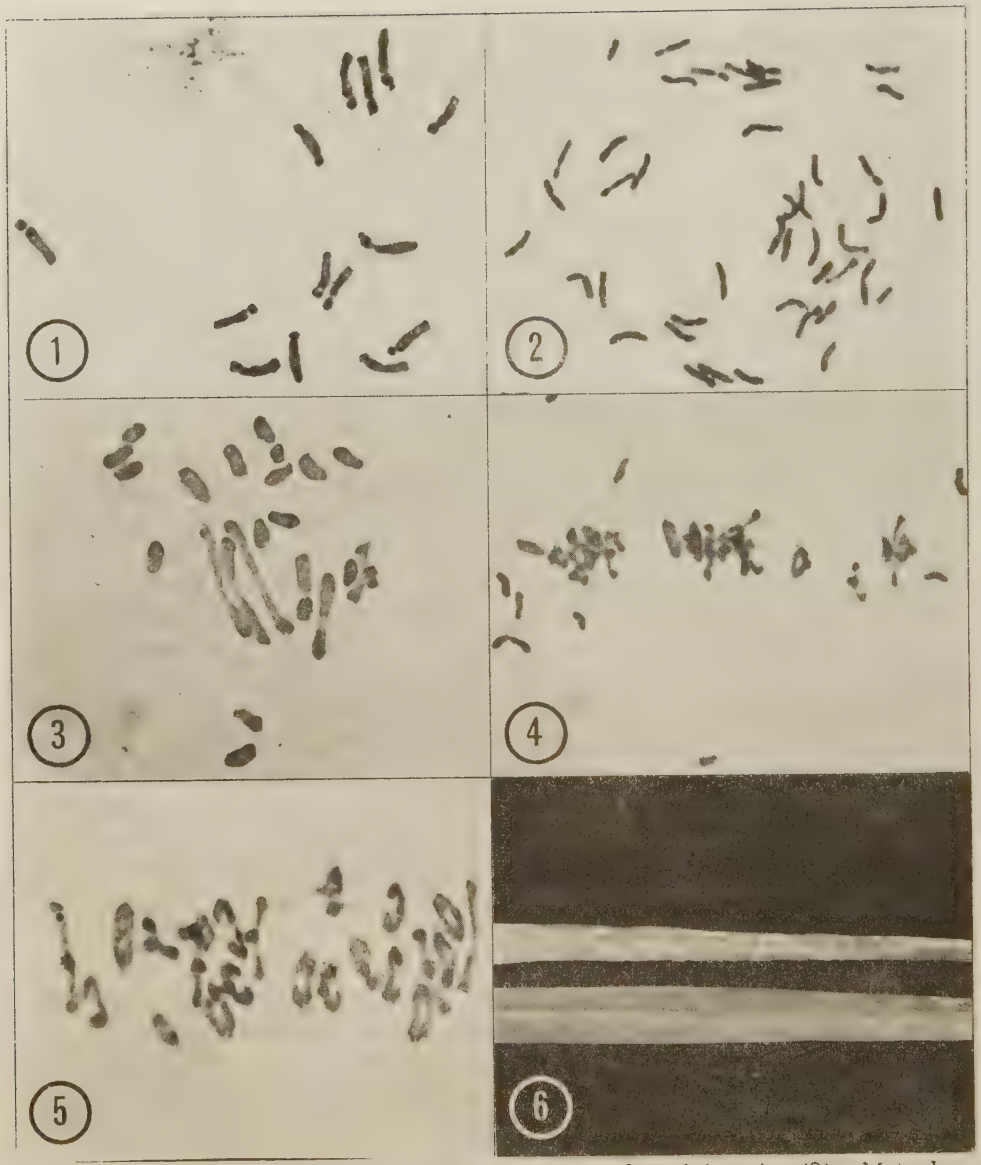


Plate 3. Somatic chromosomes of Avena ventricosa (1) and A. sativa (2). Metaphase I in: A. ventricosa x A. sativa F_1 hybrid (3); (A. ventricosa x A. sativa) x (A. hirtula x A. sativa) (4); Disomic chromosome addition line of A. hirtula chromosome to A. sativa (5). Mildew reaction of Manod oats and A. hirtula addition line (6).

References

(1) M. Borrill and C.P. Carroll, 1969. Cytologia 34, 6-17.

(2) C.P. Carroll and M. Borrill, 1965. Genetica 36, 65-82.

(3) P. Chandrasekharan, 1968. Ph.D. Thesis Univ. Wales (unpublished)

(4) John Clarke, 1969. Z. PflZucht. 62 (4), 305-310.

(5) F.M. Gauthier and R.C. McGinnis, 1968. Can. J. Genet. Cytol. 10, 186-189.

(6) D.J. Griffiths, D.G. Rowlands and W.T.H. Peregrine, 1959. Agric. Sci. 52, 189-199.

(7) Keith Jones, C.P. Carroll and M. Borrill, 1961. Cytologia 26, 333-343.

(8) Keith Jones and M. Borrill, 1962. Genetica 32, 296-322.

(9) C.P. Malik and P.T. Thomas, 1966. Caryologia 19 (2), 167-196.

(10) C.P. Malik and P.T. Thomas, 1966. Chromosoma 18, 1-18.

(11) C.P. Malik and P.T. Thomas, 1966. Z. PflZucht. 55, 81-94.

(12) C.P. Malik and P.T. Thomas, 1967. Caryologia 20 (1), 1-39.

(13) H.C. Murphy, K. Sadanaga, F.J. Zillinsky, E.E. Terrell and R.T. Smith, 1968, Science 159, 103-104.

(14) I. Nishiyama and M. Tabata, 1964. Japan J. Genet. 38, 311-316.

(15) T. Rajhathy and H. Thomas, 1967. Can. J. Genet. Cytol. 9, 52-68.

(16) T. Rajhathy, 1966. Can. J. Genet. Cytol. 8, 774-779.

(17) T. Rajhathy and R.S. Sadisavaiah, 1969. Can. J. Genet. Cytol. 11, 77-85.

(18) U.B.S. Swami and H. Thomas, 1966. Can. J. Genet. Cytol. 8, 50-56.

(19) H. Thomas and T. Rajhathy, 1967. Can. J. Genet. Cytol. 9, 154-162.

(20) H. Thomas and P.T. Thomas, 1963. Rep. Welsh Pl. Breed. Stn for 1962, 95-96.

(21) H. Thomas and D.A. Lawes, 1968. Euphytica 17, 404-413.

(22) H. Thomas and D.I.H. Jones, 1968. Nature, Lond. 220, 825-826.

(23) H. Thomas, 1968. Can. J. Genet. Cytol. 10, 551-563.

(24) H. Thomas, Can. J. Genet. Cytol. (in press).

(25) P.T. Thomas with P. Chandrasekharan, The synthesis of a stable hexaploid *Festuca pratensis* (in preparation).

PHYSICS

F.H. VANSTONE

The decision was taken in 1963 to add environmental recording to the array of techniques used in research at the Station. Up to that time the only information relevant to the climate of the Station was that available from the measurements made to enable it to fulfill its function as a Meteorological Office Agro-met. Station. These once-daily measurements provided data on the daily wind-run, sunshine hours and rainfall, maximum and minimum air and soil surface temperatures, and the relative humidity at a particular time, at a particular site. Such information was related to one specific site, and information on the climatic variation over the experimental plots was not available.

Any investigation on crop growth requires data on the intensity and duration of the light reaching the crop, transmitted down through and reflected by the crop. There is a similar requirement for all the other parameters of the immediate environment, or micro-climate, of the crop. At the commencement of this work, in the absence of such data, the breeder was unable either to relate the performance of his plants to their environment or to arrive at any estimate of their efficiency in converting solar energy into food.

Micro-climate is a dynamic entity, its parameters are rarely constant, even for a short time; they vary between widely separated values on any single day, forming a pattern which, at best, is predictable to a very limited extent, therefore spot readings, or measurements made at infrequent intervals through the day, are of little value. A detailed picture of the energy fluxes to which a crop has been subjected on a given day, can only be obtained from measurements of a number of micro-climate parameters either made at frequent intervals or from continuous sensing with periodic recording of the integrals.

The agronomist is interested in the extent to which the crop is able to create its own micro-climate, and in the relation between this micro-climate and the "local" macro-climate. Since the primary interest at the Station is in the grass crop, our measurements should also provide information in relation to agrotopoclimatological considerations in connection with this crop. So at the outset there was no question of growing "model" crops in close proximity to the laboratory buildings housing the recording equipment to which the field sensors could be connected with relative ease. Clearly, therefore, our task was to develop equipment which was self-powered and portable, and which would function and measure satisfactorily when exposed to the en-

vironment which it was to measure. The Welsh hill climate is hostile to both plant and animal and we can now say with hind sight and conviction that it is no less hostile to instruments placed in it to measure and record its parameters.

The decision to resort to self-powered, portable recording instruments having been taken, consideration of the situation with regard to sensors revealed that in general terms sensors of suitable sensitivity and dimensions were not available and so it was necessary to devote a considerable effort to the development of such equipment.

Sensors

For field measurements involving plants, replication is vital and sensors are required in large numbers, thus they should be cheap to buy or easy to produce. Light energy is probably the most important environmental parameter from the plant's point of view and so has received the greatest consideration at the Station.

Light

For light measurements in the field, suitable sensors were not available. For convenience, and in view of the urgency, attempts were made to incorporate photovoltaic elements, such as selenium and silicon cells, in light sensors. Initially this approach had many attractions, but it became clear that it would require a considerable research effort, and it was abandoned.

We are interested in the light reflected from and transmitted through the crop canopy, as well as in the incoming solar radiation. These three light components have different spectral compositions. For ease of interpretation of the data, sensors which accept the spectral range of these components should have a neutral response, i.e. should respond equally to a given input rate of light energy independently of its spectral composition. Also, for field measurements the output from the sensors is fed to transistorized amplifiers exposed to field conditions. In such conditions the performance of the amplifier is the better the lower the amplification required of it. These criteria are met by the high sensitivity multi-junction thermo-couple tube and hemispherical solarimeters produced at the Station (3).

The solarimeters are cheap in material cost, but there is a high labour component in their production. The spatial response of the tube solarimeters deviates from a cosine law by up to 15%. This is a function of the geometry of the tube, and the effect can be reduced in the case of horizontal sites by using two tubes at right angles for each measurement. But this is not a serious handicap for transmission work if observations are either confined to diffuse conditions or to planes within the crop not subject to a high incidence of sunflecks.

In view of the numbers involved, the hemispherical solarimeters have been fitted with relatively cheap general purpose glass domes. The optical quality of these domes has resulted in the spatial response deviating from a cosine law by more than 20%.

This could be completely overcome by the use of optically worked domes, but their cost is prohibitive. The sensitivity of the solarimeters, 50 $mV.cal^{-1}.cm^{-2}.min^{-1}$, is sufficiently high to permit some reduction, and so we have been able largely to overcome this defect by diffusing the domes.

The solarimeters respond to light in the wavelength range 0.4 to 3μ, i.e. the visible and near infra-red. Plants use only limited parts of this spectral range and we are endeavouring to produce solarimeters responding to specific wave bands, in the numbers necessary for field work.

Temperature

We have been fortunate in being able to use commercially available transistors as temperature sensors. The characteristics of some transistors change with temperature. This is normally a disadvantage, but in this instance we have been able to exploit this change of characteristic with temperature to our advantage. Limited experience suggests that the transistor sensor will confer no disadvantage when used with a resolution of 0.5°C.

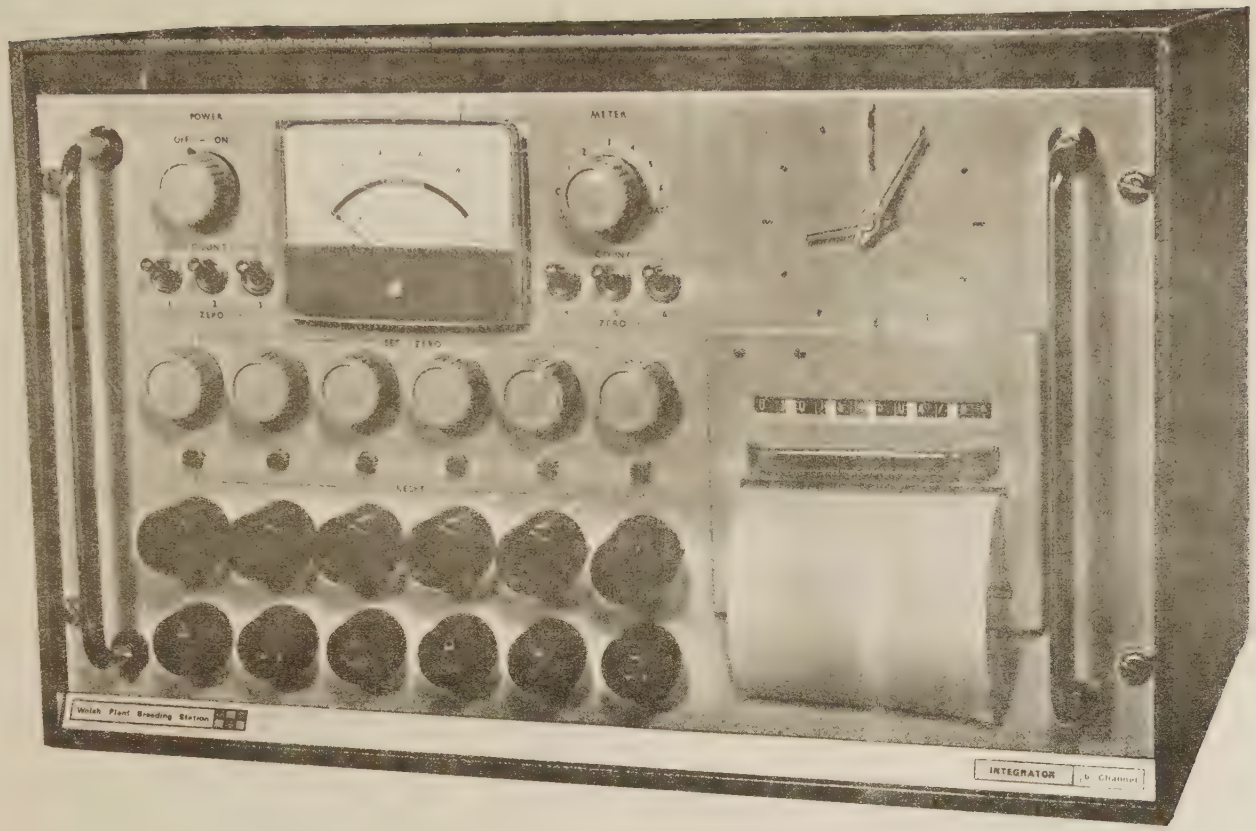
Air movement

In studies on the air movement through crops, cup-anemometers are ruled out for obvious reasons and hot-wire anemometers are used. For use with our self-powered portable instruments in remote sites the power requirement of the hot-wire is excessive and its dimensions would preclude its use with the grass crop. We propose to develop a very small sensor with very low power requirement using thermistors for such work.

Integrators

An early requirement was to provide background information on the insolation received daily on the Station experimental plots. The signal from a hemispherical solarimeter was arranged to feed a Siemens electrolytic meter (2) and the position of the bubble on the meter scale was read daily. This is a relatively crude and insensitive arrangement but a number of such units have been in operation for 5 years, and have given satisfactory information on daily integrals of insolation for all but the three winter months of each year.

Concurrently with the work on Siemens meters we set up a single channel chart recorder and fed it with the signal from a hemispherical solarimeter to provide a record of the diurnal variation of insolation. When such a recorder was fitted with a mechanical integrator, daily readings of the integrator were used to provide the "standard" daily integral of insolation received at the Station. Experience with this equipment indicated that it was quite unsuitable for daily integrals of less than 50 $cal.cm^{-2}$, and of limited use for values between 50 and 100 $cal.cm^{-2}$ which can occur for six months of the year.



Multi-channel integrator with automatic print-out

Other very simple arrangements for providing the daily insolation were produced (3) but they were all subject to some reservations. This unhappy situation was resolved by the development of a transistorized electronic integrator. Our experience with this instrument has been much happier and it has been used for some years to provide the standard Station integral.

This approach has been extended to a six-channel instrument with automatic simultaneous print-out of the integral for each channel at hourly or half-hourly intervals. Up to the present its use has been confined to the various forms of the radiation parameter, but it is our intention to arrange for its acceptance of all environmental parameters.

Data-logging

The parameters necessary for a full description of any crop environment include incoming, reflected and transmitted radiation, air, leaf surface and soil temperature, speed, run and direction of wind, air movement through the crop, water and CO_2 content of both air and soil, and rainfall. There will be mutual interactions between the crop and a number of these parameters and between some of the parameters. An understanding of these effects will depend on the ability to record the appropriate parameters at all times and at all sites.

In practice, the choice in recording these parameters is between a multi-channel chart recorder and a data-logging instrument. If we exclude extremely expensive recorders neither method will provide continuous monitoring of any parameter and we have to resort to a complete scan of all the parameters at predetermined intervals. With a multi-channel chart recorder of 12 channels, the normal scanning time is 3 to 4 minutes, with an interval of 20 seconds between sampling successive channels, so that interactions between rapidly changing parameters, such as incoming and reflected radiation, cannot be effectively studied. With data-loggers the time between sampling successive channels can be as little as 0.1 seconds, and there is much greater control and flexibility in the frequency of scanning. Further, in any multi-channel chart recording system the extraction and processing of data from the charts is an extremely time-consuming operation, which has no parallel in a data-logging system. Transducers for different parameters give different kinds of output signal so that the number of types of output signal must be matched by a similar number of chart recorders. It can be arranged for one data logger to accept any number of types of signal within the total channel capacity of the logger.

The above considerations lead to the conclusion that the only practical approach to meeting our requirements would be provided by a battery driven data-logger. Shortly after this conclusion was reached the Limpet Logger was announced. Careful consideration was given to its specification from which it appeared that the instrument would provide a satisfactory solution of our requirements and the decision was taken to incorporate the logger into our system.

The Limpet Logger has been described in detail (1) and only a very brief description will be given here. Normally the circuitry is quiescent and the only power consumption is that of a 1.5 V dry battery which provides a rewind of the clock mechanism every minute. Used for this purpose the battery life is of the order of 12 months. When the clock "calls", the channels, up to a maximum of 10, are sampled in turn and the logger circuitry operates for a period of up to 4 seconds, depending upon the number of channels being used. The time between calls can be any number of minutes up to one hour. The signal from each channel is converted into a train of pulses which is stored on a magnetic tape. When 10 channels are used and the call is made at 6-minute intervals one tape cassette will operate for 10 days. The recorded data are extracted in digital form by passing the tape through a laboratory based translator.

In common with other workers, we were forced to conclude that the production instrument was not sufficiently developed or reliable for our work. For most of the environmental recordings envisaged at the Station there appeared to be no practical alternative to the logger, but it became clear that considerable amount of development work would be necessary before the logger could be accepted for our purposes.

For mains driven equipment housed in temperature controlled laboratories there is virtually no limitation on size, weight, or power requirement. Portable equipment to be used in remote sites is limited in respect of all these factors, but the advent of semi-conductor devices to take the place of thermionic tubes has made it possible to overcome these limitations. The characteristics of semi-conductors are considerably changed by changes in temperature. So when the semi-conductor circuitry of the logger operates satisfactorily in the laboratory, it does not follow that it will do so in the wide temperature range of remote hill sites.

The Limpet logger system can be broken down into nine component parts -

(1) Input circuitry which amplifies, attenuates or rectifies the incoming signals into D.C. signals on a 0 to 5 V scale.
(2) Analogue to digital convertor which changes the 0 to 5 V D.C. signals into trains of 5 to 105 pulses.
(3) Sampling timer which controls the A-D convertor "read time" for each channel.
(4) Counter which controls the scanning of input channels.
(5) Timer which controls the frequency of scanning.
(6) Recording system which transfers the digital information to magnetic tape.
(7) Tape transport.
(8) Regulator to provide a constant voltage for the measuring circuitry.
(9) Translator which transfers the information from magnetic tape to typewriter or tape punch output, as required.

The investigation has revealed shortcomings under all these headings. As modifications have been incorporated in one section the resulting improvement has revealed a weakness in another. There is scope for further development of the system, but the logger is expected to function satisfactorily in its present form under most of the conditions to which it will be subjected. The effect of the temperature of the logger it-

self on the resolution to be ascribed to the recorded data has not yet been investigated.

Recording techniques

The mains driven chart recorder continuously recording insolation has been shown to be unsuitable for integration purposes on days of low insolation. We propose to continue its use as a recorder, as it is very convenient for a quick retrospective scan of the radiation conditions to which a crop has been subjected.

The logger provides instantaneous data on each channel at preselected intervals (every 6 or 2 min), but apart from wind and rain it provides no information on any parameter between each scan. The multi-channel integrator senses each channel continuously and prints out the respective integrals at hourly or half-hourly intervals, but under average conditions it will give no direct information on peaks or troughs during each integral period. Normally, the logger will not provide this information, but will approximate to such a requirement when its scanning frequency is increased to 15 times per minute for 10 channels, or 150 times per minute for 1 channel. In both instances it will outmatch a chart recorder with the added considerable advantage of providing a direct data output in digital form.

Detailed investigations are needed to enable us to arrive at the optimal use of each of these instruments.

References

(1) I.C.Strangeways and J.S.G.McCulloch, 1965, Bull.Int.Ass.Scient.Hydrol. 10, No.4, 57.

(2) E.S.Trickett and L.J.Moulsley, 1956, J.Agr.Eng.Res. 1, 1.

(3) F.H.Vanstone, Welsh Pl.Breed.Stn Annual Report for 1967, 135-160.

GENERAL REPORT FOR 1968 and 1969

The report on the work of the Station during 1968 and 1969 is included in the review for the past 50 years.

Agricultural Research Council Visiting Group

The Station was pleased to receive the A.R.C. Visiting Group in May 1968 to discuss the programme of work for the next six years. The Group comprised Professor O.V.S.Heath, F.R.S., Reading (Chairman); Major J.M.Dugdale, Newtown, Mont.; Professor D. Lewis, F.R.S., London; Professor N. F. Robertson, Edinburgh; Professor P.E.Weatherley, Aberdeen; they were accompanied by Mr.D. J. Parkinson, Dr. Rudd Jones and Mr.G.C.Stevenson from A.R.C.Headquarters.

The Director was grateful for the valuable advice, guidance and encouragement provided in the Group's report which was approved by the Agricultural Research Council.

Staff

The Director was awarded the C.B.E. in the 1968 New Year's Honours List.

The following appointments to the scientific staff were made during 1968 and 1969: L.R.Mytton, B.Sc., J.F.Potter, B.Sc., D.H.Hides, B.Sc. (Herbage Breeding); R.G. Simons, B.Sc., Henry Thomas, B.Sc. (Grassland Agronomy); B.C.Clifford, Ph.D., P.A.York, B.Sc., R.M.Habgood, B.Sc., R.Cook, B.Sc. (Arable Crops); P.W.Wilkins, B.Sc., P.W.Simmonds, B.Sc. (Plant Pathology) and R.W.Welch, B.Sc. (Chemistry).

The following have left the Station and have taken appointments elsewhere:- Dr.F.J.Burrows (July 1968) - Department of Biological Science, Macquarie University, New South Wales, Australia; Mr.R.G.Mayes (September 1968) - University of Leeds; Mr. Tibor Emecz (September 1968) - Soil Fertility Dunns Ltd., Corsham, Wilts; Dr. John Cotten (July 1969) - Plant Pathology Laboratory, Hatching Green, Harpenden, Herts; Mr.D.G.Miles (October 1969) - F.A.O., Beef Industry Development Project, Kenya. Other resignations among scientific staff were Mrs.A.C.Burrows and Mrs.M. J.Mee.

Miss M.E.Owen retired on 31 March 1968 after 24 years service as Clerical Officer; Mr.Enoch Jones, Farm Foreman, retired on 30 September 1968 after 38 years service, 20 of which were spent in the post of Foreman. We wish them a long and happy retirement.

The following Scientific Assistants were successful in obtaining the Higher National Certificate in Biology: J.L.Jones, D.Taylor (1968), Miss M.V.Crees, R.Davies, Miss J.W.Davies, Miss C. Evans, and J. E. Jones. Three Scientific Assistants, Miss M.V. Crees, J.L. Jones and W.H. Rushton subsequently obtained appointments as Assistant Experimental Officers.

Visits and conferences abroad

The Director was a member of a group invited in June 1968 by the East German Government to study grass seed production and seed certification in that country.

Drs. E. L. Breese, M. D. Hayward and J. Hill attended the International Genetics Congress in Japan in August 1968 and gave papers.

Dr. J. P. Cooper took part in a working meeting of the Photosynthesis Sub-Section of the International Biological Programme in Wageningen in January 1968.

Dr. C. F. Eagles gave a joint paper with Dr. K. J. Treharne at the International Congress of Photosynthesis Research in Freudenstadt, Germany, in June 1968.

Mr. T. D. Johnston gave a paper at the Eucarpia Conference held in Milan, Italy, in September 1968.

Dr. E. W. Bean visited the Laboratoire du Phytotron, Gif-sur-Yvette, and Station d'Amelioration des Plantes Fourrageres, Lusignan, France, in April 1968.

In 1969, Dr. D. J. Griffiths toured herbage seed growing areas in Canada and U.S.A. under the aegis of N.S.D.O. and inspected experimental seed fields of the Aberystwyth grass and clover varieties grown in these areas for the first time.

The Conference of the Association Francaise pour la Production Fourragere held at Versailles in February 1969 was attended by Dr. J. P. Cooper who spoke on "Les potentialites des cultures fourrageres". He also attended a technical meeting of the International Biological Programme entitled Productivity of Photosynthetic Systems, Models and Methods, held in Trebon, Czechoslovakia, in September 1969.

Lectures, conferences and demonstrations

Lectures given by members of staff to university departments, learned societies, farmers' clubs, and other organizations included: by the Director, the Worcester Grassland Society; the Aberystwyth Branch of the B.M.A.; by E. L. Breese, the John Innes Institute, University of East Anglia; the Department of Agricultural Science and Applied Biology, University of Cambridge; by J. P. Cooper, the Institute of Biology, Midlands and Scottish Branches; N.A.A.S. Plant Physiology Course; research conference of the Agricultural Land Service at Keel University; the Association of Applied Biologists; the Systematic Association; by A. J. H. Carr, J. Cotten, B. C. Clifford, J. D. Hayes and I. T. Jones, the 1st International Congress of Plant Pathologists; by A. H. Charles, the 9th British Weed Control Conference; by W. Ellis Davies and J. M. M. Munro, the White Clover Research Symposium, Belfast; by W. Ellis Davies, the Ecological Workers Group meeting in Swansea; by C. F. Eagles, the Association of Applied Biologists; the Society of Experimental Biology; by P. J. Goodman, the British Ecological Society Symposium in Sheffield; by J. D. Hayes, the Jubilee Conference of

Bucks, Berks., and Oxon Farmers; the Herefordshire Agricultural Club; by J.Hill, Population Genetics Group, Liverpool; by Roy Hughes and J.M.M.Munro, the European Grassland Federation Symposium on Hill-Land Productivity, held in Scotland; by Roy Hughes, the Herefordshire Agricultural Society; the Glamorganshire Agricultural Society; by M.D.Hayward, A.J.Wright, J.Hill, C.J.A.Samuel and Miss Alison Davies, the 157th Meeting of the Genetical Society; by D.I.H.Jones, the Agricultural Group of the Society of Chemical Industry; by Ll.I.Jones, the British Association for the Advancement of Science; by J.M.M.Munro, Farming Groups in Mid-Wales; by I. Rhodes, the Population Genetics Group of the Genetical Society; by H.M.Roberts, the West Regional Seeds Committee, Ludlow; Herbage Seeds Inspectors Course at N.I.A.B., Cambridge; by A.Troughton, the Nottingham Easter School; by Hugh Thomas, the Genetical Society Meeting in December 1969.

In 1968 the course for Herbage Seeds Crop Inspectors was again held at the Station, and a joint conference with N.A.A.S. on Improvement and Utilization of Hill Land was organized in November.

To mark the 50th Anniversary of creating the Chair of Agricultural Botany and of establishing the Welsh Plant Breeding Station, a reunion of former staff and students of the two Departments was held on 4/5 July, 1969. Among the distinguished guests at the Garden Party and Reunion Dinner were the Rt.Hon.Cledwyn Hughes, Minister of Agriculture, Mr.W.R.Jones, Chief Agricultural Adviser, Ministry of Agriculture, Fisheries and Food, Sir Ben Bowen Thomas, President of the U.C.W., Aberystwyth, Sir Gordon Cox, Secretary of the Agricultural Research Council, Principal Thomas Parry, Vice-Chancellor of the University of Wales, Dr.Kenneth Mather, Vice-Chancellor of the University of Southampton, and Professor J.H.Western, University of Leeds.

As part of the Jubilee Celebrations, representatives of the National Press were invited to the Station on 25 July to tour the experimental grounds and to discuss with members of staff the research projects and some of the current achievements.

The Director was invited to deliver the Annual Radio Lecture BBC Wales on the 10th November 1969, and he chose as his subject "Plants, Production and People".

The British Grassland Society held a Symposium on Grass and Forage Breeding at the Station in January 1969, and the Director gave an opening address. Papers were contributed by D.J.Griffiths, J.P.Cooper, E.L.Breese and E.J.Lewis, W.Ellis Davies, D.I.H.Jones and R.J.K.Walters, I.G.Williams and Roy Hughes, and T.D.Johnston.

The conference of the Eucarpia Fodder Crop Section was held at the Station on 15-17 April, 1969, and in addition to demonstrations of research work in hand, papers were given by J.P.Cooper, D.I.H.Jones and R.J.K.Walters.

Delegates attending the joint conference of the Association of Applied Biologists and the Federation of British Plant Pathologists visited the Station on 3 July. The Director was Chairman of the Plant Breeding Section meetings, and papers were de-

Photograph reproduced by courtesy of North Wales Publicity Service Ltd.

50th Anniversary reunion July 1969

Front - left to right: Sir Gordon Cox, Secretary A. R. C.; Sir Ben Bowen Thomas, President U. C. W.; The Rt. Hon. Cledwyn Hughes, Minister of Agriculture; Dr. K. Mather, Vice-Chancellor University of Southampton.

Back - left to right: Professor J.H.Western, University of Leeds; Dr. Thomas Parry, Vice-Chancellor University of Wales; Professor P.T.Thomas, Director, W.P.B.S.

livered by E.L.Breese, M.D.Hayward, H.Thomas, J.Cotten, J.P.Cooper, J.L.Stoddart, A.Troughton, A.J.H.Carr, P.L.Catherall, B.C.Clifford and J.D.Hayes. Dr.P.J.Goodman and Mr.John A'Brook acted as local secretaries and also read papers. Members of the A.R.C. Plant Virus Workers Group, who met under the auspices of the Association, visited the Plant Pathology Department the previous day.

With Professor P.F.Wareing of the Botany Department, U.C.W., Dr.J.P.Cooper organized the Symposium on Potential Crop Production in Britain, which was held in Aberystwyth in July. A joint paper by J.P.Cooper and E.L.Breese was given at the Symposium.

At the annual Exhibition of the Institute of Physics and of the Physical Society held in London in March 1969, an exhibition on Multi-Channel Infra-Red Gas Analysis Equipment for Measuring Photosynthesis and Transpiration was staged by the Department of Developmental Genetics, and on Remote Recording for Micrometeorology by the Station's Physicist, Dr.F.H.Vanstone.

A TV programme on the work of the Station was transmitted over BBC 1 national network on 6 October 1969, and during the year several members of staff were interviewed at various times in the BBC radio Farming Programmes. The work of the Station was also featured in the exhibit staged by the British Seeds Council at the Royal Smithfield Show, and at the National Eisteddfod of Urdd Gobaith Cymru (Welsh League of Youth).

Extramural activities

The Director was appointed Member of the Committee for Wales "The Countryside in 1970" under the Chairmanship of H.R.H. the Prince of Wales. He was also made a Member of the Committee for Wales of the Nature Conservancy.

Dr.D.J.Griffiths is a Member of the Executive Committee of the British Grassland Society and a member of Section M (Agriculture) of the British Association.

Dr.J.P.Cooper served on the N.E.R.C. Visiting Group to the Unit of Grassland Ecology, University of Sheffield, in 1968. In 1968 and 1969 he continued as a member of the I.B.P.National Sub-Committees on Production Processes, on the Use and Management of Biological Resources, and as member of the International Working Party on Plant Gene Pools. He also continued as member of the Nuffield Foundation Working Party on Applied Physiology. In 1969 Dr.Cooper was appointed member of the Panel on Biometeorological Instrumentation of the I.B.P. National Committee, and in the same year he was elected Fellow of the Institute of Biology.

Dr.A.H.Charles and Mr.Roy Hughes served on the Journal Committee of the British Grassland Society. Dr.Charles served on the Conference Programme Committee of the British Crop Protection Council.

Dr.A.Troughton was Chairman of the Welsh Soils Discussion Group in 1969.

Dr.P.J.Goodman was elected to the Plant Physiology Committee of the Association of Applied Biologists.

Mr.J.M.M.Munro was a member of the Hill Farming Workshop convened by the Agricultural Adjustment Unit, University of Newcastle-upon-Tyne.

Dr.E.L.Breese is a member of the Genetical Society and also served as member of the Genetical Society Programme Planning Group.

Visitors

The Station received a large number of visitors from Great Britain and many overseas countries. Among the visitors were the Hon.J.J.Astor, M.B.E., Chairman of the Agricultural Research Council, Mr.Gerald Fowler, M.P., Minister of State, Department of Education and Science, Mr. Padraig Faulkner, Minister for Lands and the Gaeltacht, Republic of Ireland, and Mr.Ivor Davies, then Parliamentary Under Secretary, Welsh Office.

Over 750 visitors, including hill farmers, N.A.A.S. and commercial advisory officers, research workers and students, were conducted round the experimental work at Pant-y-dwr Hill Centre in Radnorshire, during the two-year period.

Visiting research workers

During 1968 and 1969 the following visitors from abroad pursued further studies at the Station: P.M.Martin from the Department of Botany, University of Sydney, Australia; O.Østgard from Holt Agricultural Experimental Station, Tromsø, Norway; A.J. Pritchard from the Division of Tropical Pastures, C.S.I.R.O., Brisbane, Australia; W.Louwerse from I.B.S., Wageningen, Netherlands; S.Yasuda from Okayama University, Japan - all in Developmental Genetics; Miss D.Schmidt from the Federal Station for Agronomic Research, Nyon, Switzerland - in Plant Pathology; K.R.Pandey, F.A.O. Kathmandu, Nepal - in Grassland Agronomy; Mr. C.Y.Cho from the Rice Breeding Division, Crop Experiment Station, Suwan, Korea - in Arable Crops; Dr.T. Lawrence, Canada Department of Agriculture, Saskachewan, Canada; Miss Ruth Lindner, Consejo Superior de Investigaciones Cientificas, Pontevedra, Spain; Dr.Gonzalez-Bernaldez, Instituto de Edafologia y Biologia Vegetal, Madrid, Spain; Dr.E. Kellner, Institute for Cereals and Technical Crops, Rumania, and Mr. J.J.M.Hendricks, Max Planck Institute, Cologne, Germany - all in Herbage Plant Breeding.

Post-doctoral Fellowship

Dr.A.D.Charles-Edwards was awarded a research grant from the Agricultural Research Council for post-doctoral studies, in Developmental Genetics.

Postgraduate students

The degree of Ph.D. was awarded to the following postgraduate students:-

P. Chandrasekharan (1968)
J.M. de Jager (1968)
A. Teifion Jones (1968)
D. Wilson (1968)
M.A.P.P. Manthriratna (1969)
B.D. Patil (1969)

The degree of M.Sc. was awarded to:-
J.E. Quansah (1968)
J.B. Wonky-Appiah (1968)
Miss Anne E. Bowerman (1969)
O. Lawas (1969)
J.A. Quhaiwi (1969)
T. Tongchai Tong-Uthasri (1969)

The following are pursuing schemes of research for higher degrees:-
D.A. Benigno
I.M. Bhatti
O.A. del Castillo-Saume
Ching Chong
Miss Carolyn M. Hawkins
C. Hedley
J.C. Jackson
Miss J. James
S.H. Ong
A. Oppong
J.A. Manzano Ramos-Isquierdo
Miss Julie E. Pughe
J.E. Quansah
J.A. Quhaiwi
C.J.A. Samuel
J.E. Sheehy
C.K. Shurety
S.A. Shoyinka
J. Valentine
J.B. Wonky-Appiah
A.J. Wright

Sandwich course students

The following students from the University of Bath attended the 'sandwich course': in Developmental Genetics - D. Davis, B.G. Talbot, J.A. Timbrell; in Arable Crops - M.G. Bell.

Acknowledgements

We wish to express our thanks to the following:

Mr. J. Glyn Jones, Glan-hespin, Ruthin, for providing land for cereal cyst nematode investigations; N.I.A.B. Regional Trials Officers at N.I.A.B. centres, J.L. Jemmett and A.G. Tilley at Seale Hayne Agricultural College, Devon; M.C. Kemp and D.G. Evans at Norfolk Agricultural Station, Morley; J.H. Hague and R.J. Winfield at Headley Hall, Yorkshire. Mr. A.E. Cox, N.A.A.S., South West Sub-Centre at Starcross for organizing trials of oat segregates in three different sub-centres in the South-West. The Statistics Department and the Computer Unit, U.C.W., Aberystwyth, for help in preparing programmes for statistical analysis, and Mr. J.H. Dunwoody of the Statistical Research Service, Rothamsted, for help with various analyses. Acknowledgement is also due to the N.A.A.S. Officers for their co-operation at Pant-y-dwr Hill Centre.

It is a pleasure to acknowledge with appreciation the work of Mrs. E. Horzelska, Mr. Rhys Thomas, and their team, in producing this Report.

Summary of weather data recorded at the Agro-Met. Station, Gogerddan, Welsh Plant Breeding Station, 1968. Compiled by Mr.W.B.Evans. Deviations from the average of 16 year period 1954-69 are shown in parenthesis.

	Mean monthly temperature (°F.)							
	Maximum	Minimum	4 in. soil at 9am GMT	Sunshine hours/month	Rainfall in./month	Number of wet days (0.04 in. or over) with 16 yr. av.	Wind speed miles/hour	Radiation cal/cm^2/day
January	46.6(+1.5)	36.8(+2.3)	40.4(+1.9)	24.9(-23.5)	5.34(+1.94)	17 (13.8)	8.0	34
February	43.2(-1.7)	30.7(-2.6)	35.3(-2.6)	84.3(+10.9)	1.17(-1.07)	6 (10.8)	4.6	103
March	49.0(-0.6)	36.5(-0.2)	40.2(-0.7)	117.3(+ 0.1)	2.46(+0.23)	13 (9.6)	8.2	180
April	54.3(+0.6)	37.5(-1.9)	44.7(-1.6)	177.9(+22.9)	2.63(+0.18)	8 (10.1)	5.2	300
May	56.1(-2.8)	41.1(-3.3)	50.0(-2.8)	166.5(-18.9)	3.54(+0.74)	15 (12.2)	4.9	312
June	64.8(+0.7)	49.7(+0.4)	59.6(+0.3)	199.9(+ 2.2)	4.40(+1.39)	14 (10.7)	4.8	375
July	65.8(+0.4)	51.3(-1.7)	61.7(+0.4)	190.7(+26.4)	4.35(+0.73)	8 (12.0)	3.6	346
August	67.7(+2.2)	52.3(-0.4)	61.0(+0.4)	179.7(+17.4)	1.56(-1.99)	11 (13.3)	4.4	280
September	62.8(-0.5)	51.5(+1.9)	56.4(+0.2)	101.5(-22.8)	4.42(+0.31)	17 (13.7)	6.5	182
October	60.5(+2.3)	51.7(+5.5)	54.0(+2.2)	46.2(-45.7)	4.22(-0.31)	14 (15.5)	5.8	85
November	50.7(+0.2)	40.2(+1.3)	44.5(0.0)	57.2(- 2.2)	2.13(-1.87)	13 (15.4)	5.2	60
December	45.0(-2.1)	33.2(-2.5)	39.1(-1.7)	46.4(- 0.9)	2.55(-1.68)	9 (16.5)	4.8	40
Annual	55.5(0.0)	42.7(-0.1)	48.9(-0.3)	1392.5(-34.3)	38.77(-1.40)	145 (153.6)	5.5	

Temperature. A mild January was followed by below average temperature until end of May. A near average summer temperature was followed by an above average October. The year terminated with a cold December.

Rainfall. During the first seven months February was the only month with below average rainfall. During this period the total rainfall was 4 in. above average with a normal number of wet days. The rest of the year, however, was drier than average and ultimately the annual total turned out to be 1.40 in. below average.

Sunshine. With the exception of January and May the sunshine was above average until end of August. Thereafter the sunshine was lower than average, that of September and October being as much as 32% below average. The sunshine during October was the lowest recorded at the Station.

Summary of weather data recorded at the Agro-Met. Station, Gogerddan, Welsh Plant Breeding Station, 1969. Compiled by Mr. W. B. Evans. Deviations from the average of 16 year period 1954-69 are shown in parenthesis.

	Mean monthly temperature (°F.)			Sunshine hours/month	Rainfall in./month	Number of wet days (0.04 in. or over) with 16 yr. av.	Wind speed miles/hour	Radiation cal/cm^2/day
	Maximum	Minimum	4 in. soil at 9am GMT					
January	47.6(+1.5)	38.7(+4.2)	41.0(+2.5)	28.2(-20.2)	5.04(+1.64)	17 (13.8)	6.3	35
February	40.8(-4.1)	29.3(-4.0)	35.6(-2.3)	54.6(-18.8)	2.24(0.00)	13 (10.8)	6.1	91
March	46.5(-3.1)	33.7(-3.0)	38.2(-2.7)	115.5(- 1.7)	2.10(-0.13)	6 (9.6)	5.6	167
April	52.9(-0.8)	38.0(-1.4)	44.5(-1.8)	201.5(+46.5)	2.04(-0.41)	7 (10.1)	6.9	308
May	58.3(-0.6)	45.0(+0.6)	51.4(-1.4)	133.7(-51.7)	7.15(+4.35)	22 (12.2)	5.0	274
June	64.7(+0.6)	47.1(-2.2)	58.9(-0.4)	268.2(+70.5)	2.06(-0.95)	9 (10.7)	5.4	449
July	66.6(+1.2)	52.8(+0.2)	62.3(+1.0)	168.2(+ 3.9)	1.97(-1.65)	6 (12.0)	4.5	332
August	66.3(+0.8)	53.6(+0.9)	60.8(+0.2)	131.7(-30.8)	4.93(+1.38)	12 (13.3)	4.7	252
September	63.7(+0.4)	50.1(+0.5)	57.2(+1.0)	84.9(-39.4)	1.78(-2.33)	7 (13.7)	4.1	174
October	62.3(+4.1)	50.2(+4.0)	53.5(+1.7)	106.8(+14.9)	1.92(-2.61)	10 (15.5)	4.9	124
November	49.2(-1.3)	37.5(-1.4)	43.0(-1.5)	55.3(- 4.1)	6.03(+2.03)	21 (15.4)	6.8	60
December	44.7(-2.4)	33.2(-2.5)	38.7(-2.1)	39.8(- 7.5)	4.28(+0.05)	18 (16.5)	5.7	37
Annual	55.3(-0.2)	42.4(-0.4)	48.8(-0.5)	1388.4(-38.4)	41.54(+1.37)	148 (153.6)	5.5	

Temperature. A mild January was followed by a very cold late spring. Summer temperature was average or slightly above average. October was well above average with a maximum temperature of 71° on 17th. The year terminated with below average temperature in November and December.

Rainfall. Following a wet January the spring months were average or below average. Rainfall during May was the highest recorded in the district since observations commenced at the near-by Frongoch Agro. Met. Station in 1924. A dry autumn was sandwiched between the wet months of August and November.

Sunshine. During eight months the sunshine was below average. January to March and August and September were 17% and 25% below average respectively. April and June were the only months with above average sunshine.

CONVERSION FACTORS

Mass

1 g = 0.0022 lb = 0.035 oz
1 kg = 2.20 lb = 35.3 oz
1 t (tonne) = 1000 kg = 0.984 tons
(1.102 tons)*

1 oz = 28.35 g
1 lb = 453.6 g = 0.45 kg
1 cwt = 50.80 kg
(1 cwt = 45.36 kg)*
1 ton = 1016.0 kg = 1.016 t
(1 ton = 907.2 kg = 0.907 t)*

Linear

1 mm = 0.039 in.
1 m = 1.09 yd = 3.28 ft
1 km = 1094 yd = 0.62 miles

1 in. = 25.4 mm
1 ft = 0.305 m
1 yd = 0.914 m
1 mile = 1.61 km

Area

1 cm^2 = 0.155 in^2 = 0.00108 ft^2
1 m^2 = 10.76 ft^2 = 1.20 yd^2
1 km^2 = 0.386 $miles^2$ = 247 acres
1 ha = 10000 m^2 = 2.47 acres

1 in^2 = 6.45 cm^2
1 ft^2 = 0.093 m^2
1 yd^2 = 0.836 m^2
1 acre = 4,047 m^2 = 0.4047 ha

Capacity and Volume

1 cm^3 = 0.061 in^3
1 m^3 = 35.31 ft^3 = 1.31 yd^3
1 litre = 1.76 pints = 0.22 gall

1 in^3 = 16.39 cm^3
1 ft^3 = 28.3 litres = 28316 cm^3
1 yd^3 = 0.765 m^3
1 pint = 0.57 litres
1 gallon = 4.55 litres

Combined units

1 kg/ha = 0.892 lb/acre
1 t/ha = 892 lb/acre
= 0.398 ton/acre
= (0.446 ton/acre)*
1 g/m^2 = 8.92 lb/acre

1 lb/acre = 1.12 kg/ha = 0.112 g/m^2
1 cwt/acre = 125.5 kg/ha = 0.126 t/ha
(1 cwt/acre = 112.1 kg/ha = 0.112 t/ha)*

1 ton/acre = 2.51 t/ha
(1 ton/acre = 2.24 t/ha)*

Temperature

-10	-5	0	5	10	15	20	25	30	°C
14	23	32	41	50	59	68	77	86	°F

Light intensity

1 lux = 0.093 ft-candle
1000 ft-candles = 10,763 lux = 0.057-0.072 $cal/cm^2/min$† = 40-50 W/m^2†

* American measures
† of visible radiation; exact values depend on the spectral distribution.

PUBLICATIONS

A'BROOK, J. 1968. The effect of plant spacing on the numbers of aphids trapped over the groundnut crop. Ann. appl. Biol. 61, 289-294.

BEAN, E.W. 1968. Inflorescence production in the amphiploid Lolium multiflorum (2n = 28) x Festuca arundinacea (2n = 84). Euphytica 17, 479-484.

_____. 1969. Environmental and genetic effects upon reproductive growth in tall fescue (Festuca arundinacea Schreb.). J. agric. Sci., Camb. 72, 341-350.

BEDDOWS, A.R. 1968. Head emergence in forage grasses in relation to February-May temperatures and the predicting of early or late springs. J. Br. Grassld Soc. 23, 88-97.

_____, 1968. A history of the introduction of timothy and cocksfoot into alternate husbandry in Britain. 1. The year 1763 and its significance. J. Br. Grassld Soc. 23, 317-321.

_____, 1969. A history of the introduction of timothy and cocksfoot into alternate husbandry in Britain. 2. The impact of timothy on ley farming. J. Br. Grassld Soc. 24, 40-44. 3. The impact of cocksfoot on ley farming. J. Br. Grassld Soc. 24, 163-167.

_____, 1969. Skew distribution of panicle-emergence dates in populations of cock's-foot, Dactylis glomerata L. (Gramineae). Biol. J. Linn. Soc. 1, 287-292.

_____, 1969. Observations on the flowering of fruit trees. Scient. Hort. 21, 132-140.

BORRILL, M. with PARKER, P.F. 1968. Studies in Dactylis. I. Fertility relationships in some diploid subspecies. New Phytol. 67, 649-662.

_____, and CARROLL, C.P. 1969. A chromosome atlas of the genus Dactylis. Cytologia 34, 6-17.

_____, with BENSON, Maureen 1969. The significance of clinal variation in Dactylis marina Borrill. New Phytol. 68, 1159-1173.

BOWERMAN, Anne, E. 1969. The physiology and genetics of nitrate reductase activity in Lolium spp. M.Sc. Thesis Univ. Wales (unpublished).

BREESE, E.L. 1968. Improving Britain's grassland output. Herbage breeding aims surveyed. Span 11 (3), 162-165.

_____, 1968. Population structure of ecotypes. Proc. XII Int. Congress of Genetics, Tokyo, 1968. Vol.2, p.218-219.

_____, 1969. The measurement and significance of genotype environment interactions in grasses. Heredity, Lond. 24, 27-44.

_____, and LEWIS, E.J. 1969. Grasses - species and hybrids. Grass and Forage Breeding. Occ.Symp.No.5, Br.Grassld Soc. 15-20.

_____, with JINKS, J. L. and PERKINS, Jean, M. 1969. A general method of detecting additive, dominance and epistatic variation for metrical traits. II. Application to inbred lines. Heredity, Lond. 24, 45-57.

BURROWS, A.C. with JONES, D.Gareth 1968. Breeding for increased nodule tissue in white clover (Trifolium repens L.). J.agric.Sci., Camb. 71, 73-79.

_____, with _____, 1969. Acid production and symbiotic effectiveness in Rhizobium trifolii. Soil Biol. and Biochem. 1, 57-61.

CARR, A.J.H. 1968. Virus diseases of grasses. Span 11 (2), 92-95.

_____, 1968. Investigations on virus diseases of grasses. Eucarpia, Fodder Crop Section, Report of meeting, September 1967, 51-55.

CHANDRASEKHARAN, P. 1968. Cytogenetics of synthetic derivatives of Lolium-Festuca. Ph.D.Thesis Univ.Wales (unpublished).

CHARLES, A.H. 1968. Some selective effects operating on white and red clover in swards. J.Br.Grassld Soc. 23, 20-25.

_____, 1968. Weed control in grass and legume forage crops and natural grassland. In: Weed Control Handb. Chaper 11, Vol.1, 5th edition. Eds.J.D. Fryer and S.A.Evans, London, Blackwell Scientific Publications, pp.255-272.

_____, 1968. Control of weed grasses by the selective effects of fertilizer applications and management. Proc.9th Br.Weed Control Conf. 1968, Brighton. Vol.III, 1223-1230.

CLARKE, John 1969. The use of 5-aminouracil for synchronizing nuclear division as a pre-treatment for the production of polyploids in Lolium. Z.PflZucht., 62, 305-310.

CLIFFORD, Brian C. and SCHAFER, John F. 1968. Effects of host resistance-type on population dynamics of Puccinia coronata avenae. University of Manchester. Study Conference on leaf and ear diseases of cereals, April 1968 (mim.).

CLIFFORD, Brian C. and SCHAFER, John F. 1968. Non-race specific resistance of Avena sativa L. to Puccinia coronata Cda var. avenae F. and L. Proc. First Int. Congr. of Plant Pathology, London 1968. p.32 (Abstract).

COOPER, J.P. 1968. Yr heulwen, y cnydau a ninnau. Y Gwyddonydd Cyfrol 6: Rhifyn 2 : Gwasg Prifysgol Cymru : Mehefin : 1968.

_____, and TAINTON, N. M. 1968. Light and temperature requirements for the growth of tropical and temperate grasses. Herb. Abstr. 38, 167-176.

_____, with TAYLOR, T. H. and TREHARNE, K. J. 1968. Growth response of orchard-grass (Dactylis glomerata L.) to different light and temperature environments. I. Leaf development and senescence. Crop Sci. 8, 437-440.

_____, 1969. Potential forage production. Grass and Forage Breeding. Occ. Symp. No.5, Br. Grassld Soc. 5-13.

_____, 1969. Potentialites des productions fourrageres. Fourrages, No.38, 3-19.

_____, 1969. Variation in physiological characters influencing production of forage grasses. Eucarpia, Fodder Crop Section, Report of meeting, April 1969. 9-16.

COTTEN, John and HAYES, J.D. 1969. Genetic resistance to the cereal cyst nematode (Heterodera avenae Woll.). Heredity, Lond. 24, 593-600.

DAVIES, Alison 1968. The growth of grass in spring. N.A.A.S.q.Rev. 79, Spring 1968. pp.98-100. Reprinted in Herbivaria No.7, Jan.1969, 9-11.

_____, and CALDER, D.M. 1969. Patterns of spring growth in swards of different grass varieties. J. Br. Grassld Soc. 24, 215-225.

DAVIES, W. Ellis, THOMAS, T.A. and YOUNG, Norman R. 1968. The assessment of herbage legume varieties. III. Annual variation in chemical composition of eight varieties. J. agric. Sci., Camb. 71, 233-241.

_____, 1969. Herbage legumes - special considerations. Grass and Forage Breeding. Occ. Symp. No.5, Br. Grassld Soc. 21-27.

_____, 1969. The potential of Lotus spp. for hill land in Wales. J. Br. Grassld Soc. 24, 264-270.

_____, 1969. The assessment of herbage legume varieties. IV. The potential of 64-chromosome white clover. J. agric. Sci., Camb. 73, 139-144.

DAVIES, W. Ellis 1970. White clover breeding. Review. White Clover Research Symposium 1969. Occ.Symp.No.6, Br.Grassld Soc. 99-122.

EAGLES, C.F. 1969. Time changes of relative growth rate in two natural populations of Dactylis glomerata L. Ann.Bot.N.S. 33, 937-946.

_____, and TREHARNE, K.J. 1969. Photosynthethetic activity of Dactylis glomerata L. in different light regimes. Photosynthetica 3, 29-38.

_____, and WILLIAMS, D. H. 1969. Effect on environment on competitive ability of two natural populations of Dactylis glomerata L. J.agric.Sci., Camb. 72, 271-272.

FOSTER, C.A. 1969. The influence of planting date on the seed-bearing capacity of tillers of perennial ryegrass spaced plants grown for seed. J.Br.Grassld Soc. 24, 271-276.

_____, 1969. Efficacy of selective gametocides on Lolium perenne L. Ann. Bot. N.S. 33, 947-950.

GOODMAN, P. J. 1968. Physiological analysis of the effects of different soils on sugar beet crops in different years. J.appl.Ecol. 5, 339-357.

_____, 1969. Intra-specific variation in mineral nutrition of plants from different habitats. B.E.S.Symposium No.9. Ecological Aspects of the Mineral Nutrition of Plants. Ed.I.H. Rorison, Oxford and Edinburgh, pp.237-253 Blackwell Scientific Publications.

_____, 1969. Spartina Schreb. J.Ecol. 57, 285-287.

_____, BRAYBROOKS, E. M., MARCHANT, C. J. and LAMBERT, J. M. 1969. Spartina x townsendii (H. and J. Groves) sensu lato. J.Ecol. 57, 298-313.

_____, with MARCHANT, C.J. 1969. Spartina maritima (Curtis) Fernald. J. Ecol. 57, 287-291.

_____, with _____, 1969. Spartina alterniflora Loisel. J.Ecol. 57, 291-295.

_____, with _____, 1969. Spartina glabra Muhl. J.Ecol. 57, 295-297.

GRIFFITHS, D.J. 1969. Break crops for wheat and barley in Western Europe. Span 12, No.1, 15-18.

_____, 1969. Seed production and herbage breeding. Grass and Forage Breeding. Occ.Symp.No.5, Br.Grassld Soc. 67-73.

HAYES, J.D. 1968. The genetic basis for hybrid barley production and its application in Western Europe. Euphytica 17 (1968 Suppl.1) 87-102.

_____, 1968. Breeding and selection of nematode resistant varieties. Proc. 1st Int. Congress of Plant Pathology, London 1968. p.81 (Abstract).

_____, and HANNA, A.S. 1968. Genetic studies in field beans Vicia faba L. III. Variation in self-fertility in a diallel cross. Z.PflZucht. 60 (4), 315-326.

_____, and JONES, I.T. 1968. Race specific and non-race specific host resistance to Erysiphe graminis f.sp. avenae. Proc. 1st Int. Congress of Plant Pathology, London, 1968. p.82 (Abstract).

_____, CATHERALL, P. L. and JONES, A. T. 1969. Problems encountered in BYDV tolerant European cultivars of barley. Proc. 2nd Int. Barley Genetics Symposium, Pulman, Washington State, U.S.A.

_____, and COTTEN, J. 1969. Breeding for nematode resistance with particular reference to Heterodera avenae Woll. Proc. 2nd Int. Barley Genetics Symposium, Pulman, Washington State, U.S.A.

HAYWARD, M.D. 1968. The genetic control of adaptation in local populations of Lolium perenne L. Proc. XII Int. Congr. Genetics, Tokyo 1968, Vol.1, p.271.

_____, and BREESE, E.L. 1968. The genetic organisation of natural populations of Lolium perenne L. III. Productivity. Heredity, Lond. 23, 357-368.

_____, and NSOWAH, G.F. 1969. The genetic organisation of natural populations of Lolium perenne. (iv) Variation within populations. Heredity, Lond. 24, 521-528.

HILL, J. with ALANIS, L. BUCIO 1967. Estimating the components of genotype-environment interactions. Heredity, Lond. 22, 616 (Abstract).

_____, and PERKINS, Jean M. 1968. Predicting performance in the presence of genotype-environment interactions. Proc. XII Int. Congr. Genetics, Tokyo 1968, Vol.1, p.270 (Abstract).

_____ and _____, 1969. The environmental induction of heritable changes in Nicotiana rustica. Effects of genotype-environment interactions. Genetics 61, 661-675.

HUGHES, Roy 1968. Climatic limitations to quality hay. Rep. Welsh Pl. Breed. Stn for 1967, 161-166.

_____, 1969. Book review: Grasslands of the Monsoon by R.D. Whyte. New Scientist, 41, No.641, 648.

HUGHES, Roy and MUNRO, J.M.M. 1969. Climatic and soil factors in the hills of Wales in relation to the breeding of special herbage varieties. Hill Land Productivity. Occ.Symp.No.4, Br.Grassld Soc. 109-112.

de JAGER, J.M. 1968. Carbon dioxide exchange and photosynthetic activity in forage grasses. Ph.D.Thesis Univ.Wales (unpublished).

_____, and CHARLES-EDWARDS, Jennifer 1969. Thermal conductivity probe for soil moisture determinations. J.exp.Bot. 20, 46-51.

JOHNSTON, T.D. 1968. Studies on a diallel cross and double-cross hybrids among various Brassica oleracea types. Euphytica 17, 63-73.

_____, 1968. Clubroot disease in Brassica: A standard inoculation technique and the specification of races. Pl.Path. 17, 184-187.

_____, 1968. Book review: Induced Mutations and their Utilization. Proc.4th Erwin Baur Symposium, ed. H.Stubbe. Heredity, Lond. 23, 457-458.

_____, 1969. The forage Brassicae - achievements and prospects. Grass and Forage Breeding. Occ.Symp.No.5, Br.Grassld Soc. 83-87.

_____, 1969. Book review: Plant Breeding. Studies in Biology No.12 by William J.C.Lawrence. Sci.Progr. 57, No.227, 451-453.

JONES, A.Teifion 1968. Factors affecting the expression of tolerance in cereals to barley yellow dwarf virus. Ph.D.Thesis Univ.Wales (unpublished).

JONES, D.I.H. and ap GRIFFITH, G. 1968. Microwave drying of herbage. J.Br. Grassld Soc. 23, 202-205.

_____, and WALTERS, R.J.K. 1969. Varietal variation in nutritive characteristics. Grass and Forage Breeding. Occ.Symp.No.5, Br.Grassld Soc. 37-43.

_____ and _____, 1969. The problem of assessing quality in the breeding of forage plants. Eucarpia, Fodder Crop Section, Report of Meeting April 1969, pp.57-66.

_____, with SINCLAIR, K.B. 1968. Comparison of the weight gain and the composition of blood saliva in sheep grazing timothy and ryegrass swards. Br.J. Nutr. 22, 661-666.

JONES, I.T. 1968. Studies on mature plant resistance in oats to Erysiphe graminis avenae. Abstract - Study Conference on leaf and ear diseases of cereals. Manchester University, April 1968, pp.1-2 (mim.).

JONES, I.T. and HAYES, J.D. 1968. The effect of seed rate and growing season on four oat cultivars. II. Culm morphology and panicle conformation. J. agric. Sci., Camb. 70, 405-410.

LAWAS, O. 1969. Some effects of phosphate, light and other factors on growth and yield of Lolium perenne L. and Lolium multiflorum Lam. M.Sc.Thesis Univ. Wales (unpublished).

LAWES, D. A. 1968. Crop husbandry and the yield of cotton in Northern Nigeria. Cott.Gr.Rev. 45, 1-16.

LEWIS, J. 1968. Fertile tiller production and seed yield in meadow fescue (Festuca pratensis L.). II. Drill spacing and date of nitrogen manuring. J.Br.Grassld Soc. 23, 240-246. III. Date of spring defoliation and nitrogen application. J. Br.Grassld Soc. 24, 50-58.

MANTHRIRATNA, M.A.P.P. 1969. The cyto-physiology of rye-grass pollen. Ph. D.Thesis Univ.Wales (unpublished).

MILES, D. G., WALTERS, R. J. K. and EVANS, E. M. 1969. Dry-matter intake and live-weight gain of cattle and sheep offered different grass varieties with and without clover. Anim.Prod. 11, 19-28.

MUNRO, J.M.M. 1967. Soil limitations in the reseeding of hill land. Welsh Soils Disc.Group, Rep.No.8, 1967, 88-95.

_____ and HUGHES, Roy. 1968. The evaluation of herbage varieties in hill-land conditions. Hill Land Productivity. Occ.Symp.No.4, Br.Grassld Soc. 113-117.

_____, 1969. Objectives in hill land research. J.agric.Soc.Univ.Coll.Wales, Aberystwyth, 49, 15-19.

_____, 1970. The role of white clover in hill areas. White Clover Research Symposium 1969. Occ.Symp.No.6, Br.Grassld Soc. 259-266.

PARKER, P.F. 1968. Genetic variation in diploid Dactylis. I. Cross compatibility and seedling characters. Heredity, Lond. 23, 279-300. II. Emergence date and some morphological and physiological leaf characters. Heredity, Lond. 23, 369-386.

PATIL, B.D. 1969. Genetic variation in herbage species with respect to animal performance. Ph.D.Thesis Univ.Wales (unpublished).

_____, JONES, D. I. H. and HUGHES, Roy 1969. Wool characteristics as an indication of nutritive attributes in herbage varieties. Nature, Lond. 223, No. 5210, 1072-1073.

PHILLIPS, LL. 1969. The Welsh Plant Breeding Station. Agriculture, Lond. 76, No. 10, 479-482.

_____, 1969. Diwrnodau'r Tir. Royal Welsh 1968-69, 30-31.

QUANSAH, J. E. 1968. Studies in resistance to two diseases in Cruciferae. M.Sc. Thesis Univ.Wales (unpublished).

QUHAIWI, J.A. 1969. The effect of soil moisture stress on the development and yield of four cereal varieties. M.Sc.Thesis Univ.Wales (unpublished).

RHODES, I. 1967. The growth and development of Phalaris coerulescens Desf. C.S.I.R.O Field Station Record 6, 69-76.

_____, 1968. Studies on the effects of competitive stress on the growth and development of some grass speices and populations. J.Aust.Inst.agric.Sci. 34, 223.

_____, 1968. The growth and development of some grass species under competitive stress. 1. Competition between seedlings, and between seedlings and established plants. J.Br.Grassld Soc. 23, 129 136. 2. Regrowth, floral development and seasonal production. J.Br.Grassld Soc. 23, 247 258. 3. The nature of the competitive stress, and characters associated with competitive ability during seedling growth. J.Br.Grassld Soc. 23, 330-335.

_____, 1968. Advance note on research. Yield of contrasting ryegrass varieties in monoculture and mixed culture. J.Br.Grassld Soc. 23, 156-158.

_____, 1969. The yield, canopy structure and light interception of two ryegrass varieties in mixed culture and monoculture. J.Br.Grassld Soc. 24, 123-127.

_____, 1969. The relationship between productivity and some components of canopy structure in ryegrass (Lolium spp.). I. Leaf length. J.agric.Sci., Camb. 73, 315-319.

ROBERTS, H.M. 1968. Production and sale of good cereal seed. W.A.O.S.Bulletin Farmer Business in Wales, No.9, Winter 1968/69, p.15 and 18.

_____, 1969. Harvesting S.352 timothy for seed. J.Br.Grassld Soc. 24, 14-16.

SAMUEL, C.J.A., HILL, J. and DAVIES, Alison 1968. Genetic assessment of Lolium perenne in different environments. Heredity, Lond. 23, 624 (Abstract).

SANT, F.I. 1969. A comparison of the morphology and anatomy of seedling leaves of Lolium multiflorum Lam. and L.perenne L. Ann.Bot.N.S. 33, 303-313.

STODDART, J.L. 1968. The association of gibberellin-like activity with the chloroplast fraction of leaf homogenates. Planta (Berl.), 81 (1), 106-112.

_____, 1968. Biochemical aspects of seed ripening in grasses. J.natn Inst. agric.Bot. 11, 370-377.

_____, and LANG, A. 1968. Gibberellin synthesis in red clover. Plant Research 1967. Ann.Rep.Michigan State Univ., Atomic Energy Commission, Plant Research Laboratory, pp.44-46.

_____, 1969. Incorporation of kaurenoic acid into gibberellins by chloroplast preparations of Brassica oleracea. Phytochemistry 8, 831-837.

_____, and LANG, A. 1969. The effect of daylength on gibberellin synthesis in leaves of red clover (Trifolium pratense L.). In: Biochemistry and Physiology of Plant Growth Substances. pp.1371-1383. Proc.6th Int.Conf.on Plant Growth Substances, Ottawa 1967.

SWAMI, U. B. S. and THOMAS, Hugh 1968. Chromosme pairing in autotetraploid Avena. Z.PflZucht. 59, 163-170.

THOMAS, Hugh and RAJHATHY, Tibor 1967. Chromosomal differentiation and speciation in diploid Avena. III. Mediterranean wild populations. Can.J.Genet. Cytol. 9, 52-68.

_____, 1968. The addition of single chromosomes of Avena hirtula to the cultivated hexaploid oat A.sativa. Can.J.Genet.Cytol. 10, 551-563.

_____, 1968. Meiosis in the Avenae. In: The Effect of Ionizing Radiations on Meiotic Systems. Panel Proc.Series Int.Atomic Energy Agency, Vienna 1968, 169-172.

_____, and JONES, D.I.H. 1968. Electrophoretic studies of proteins in Avena in relation to genome homology. Nature, Lond. 220 (5169), 825-826.

_____, and LAWES, D.A. 1968. Evaluation of the use of species hybrids and synthetic amphiploids in the improvement of the oat crop. Euphytica 17, 404-413.

THOMAS, P.T. 1967. The Welsh Plant Breeding Station. Seeking grass for intensive production. Express and Times Gazette, February 11, 1967 also separate leaflet, pp.7.

_____, 1969. Herbage breeding. Grass and Forage Breeding. Occ.Symp. No.5, Br.Grassld Soc., 1-4.

THOMAS, P.T. 1969. Plants, Production and People. Broadcast on BBC Wales, 10 November, 1969. BBC Publications, pp.28.

THOMAS, R.L. 1969. Interpopulation variation in perennial ryegrass. 2. Population variance coefficients. Heredity, Lond. 24, 85-90.

_____, 1969. Interpopulation variation in perennial ryegrass. 3. Interaction of heritable and environmental variation. Heredity, Lond. 24, 91-100.

TONGUTHAISRI, Tongchai 1969. Cross compatibility between diploid and tetraploid perennial ryegrass (Lolium perenne L.). M.Sc.Thesis Univ.Wales (unpublished).

TREHARNE, K.J., COOPER, J.P. and TAYLOR, T.H. 1968. Growth response of orchardgrass (Dactylis glomerata L.) to different light and temperature environments. II. Leaf age and photosynthetic activity. Crop Sci. 8, 441-445.

_____, and STODDART, J.L. 1968. Effects of gibberellin on photosynthesis in red clover (Trifolium pratense L.). Nature, Lond. 220 (5166), 457-458.

_____, and COOPER, J.P. 1969. The effect of temperature on the activity of carboxylases in tropical and temperate Gramineae. J.exp.Bot. 20, 170-175.

_____, and EAGLES, C.F. 1969. Effect of growth at different light intensities on photosynthetic activity of two contrasting populations of Dactylis glomerata L. In: Progress in Photosynthesis Research. Ed.Helmut Metzner, Thubingen, pp. 377-382.

_____, with WAREING, P.F. and KHALIFA, M.M. 1969. Rate-limiting processes in photosynthesis at saturating light intensities. Nature, Lond. 220 (5166), 453-457.

TROUGHTON, Arthur 1968. Grass roots, their morphology and relationship with the shoot system (also in Russian translation). In: Methods of Productivity Studies in Root Systems and Rhizophere Organisms. Int.Symp.USSR August 28-September 12, 1968. p.213-220. Publ.House 'Nauka', Leningrad, USSR.

_____, 1968. Influence of genotype and mineral nutrition on the distribution of growth within plants of Lolium perenne grown in soil. Ann.Bot.N.S. 32, 411-423.

_____, and WHITTINGTON, W.J. 1968. The significance of genetic variation in root systems. Proc.15th Easter Sch.Agric.Sci.Univ.Nott., 1968. Ed. W.J. Whittington, Butterworths, London, 296-314.

TYLER, B.F., DAVIES, I. and LORENZETTI, F. 1969. Forage plant collection; an expedition to northern Italy. Rivista di Agronomia, III (No.1), 43-50.

WILLIAMS, I.G. and HUGHES, Roy 1969. Evaluating grasses and clovers in a plant breeding station. Grass and Forage Breeding. Occ.Symp.No.5, Br.Grassld Soc., 53-65.

WILSON, D. 1968. Growth and assimilation in Lolium. Ph.D.Thesis Univ.Wales (unpublished).

_____, and COOPER, J.P. 1969. Apparent photosynthesis and leaf characters in relation to leaf position and age, among contrasting Lolium genotypes. New Phytol. 68, 645-655.

_____, and _____, 1969. Effect of light intensity and CO_2 on apparent photosynthesis and its relationship with leaf anatomy in genotypes of Lolium perenne L. New Phytol. 68, 627-644.

_____, and _____, 1969. Diallel analysis of photosynthetic rate and related leaf characters among contrasting genotypes of Lolium perenne. Heredity, Lond. 24, 633-649.

_____, and _____, 1969. Effect of temperature during growth on leaf anatomy and subsequent light-saturated photosynthesis among contrasting Lolium genotypes. New Phytol. 68, 1115-1123.

_____, and _____, 1969. Effect of light intensity during growth on leaf anatomy and subsequent light-saturated photosynthesis among contrasting Lolium genotypes. New Phytol. 68, 1125-1135.

_____, and _____, 1969. Assimilation rate and growth of Lolium populations in the glasshouse in contrasting light intensities. Ann.Bot.N.S. 33, 951-965.

_____, TREHARNE, K.J., EAGLES, C.F. and de JAGER, J.M. 1969. A manometric technique for determination of apparent photosynthesis of Lolium. J.exp. Bot. 20, 373-380.

WONKYI-APPIAH, J.B. 1968. Genetic variation in photosynthetic activity and other leaf characters in Lolium perenne and Lolium multiflorum. M.Sc.Thesis Univ. Wales (unpublished).